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Morphological Characters of some Sphaeropsidales in Culture

with reference to classification

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W. Andrew Archer.

(With Plates I—VIII.)

The pycnidial stage in the life history of the ascomycetes ordinarily classified as the *Sphaeropsidales*, is known to be quite variable in the individual forms as it develops under the varying conditions present at one time or another in nature. This has resulted in endless confusion of forms, when, at different times, students have set up new genera and species in the group; — genera and species which have too often proved to be merely different aspects of one and the same fungus. Therefore, a study was attempted of the variability of as many species of the *Sphaeropsidales* as possible, and of their behavior on a standard medium and under standard conditions, in order to determine to what extent reliable morphological characters, constant under such conditions, could be found. With such data it should be possible to make suggestions for a more logical and accurate classification than is at present available.

Too often the mycologist and the plant pathologist have not fully appreciated the true nature of specific fungi. The difficulty has been that neither our conceptions nor our schemes of classification have been flexible enough to take into consideration the inherent potentialities of fungi. Fungi are not to be considered merely as immutable things but rather as living entities, which, at various times, present entirely different appearances in response to certain stimuli. It is because of the variability that the present system of species and genera of fungi based merely on formal herbarium characters is artificial and inadequate.

Evidently a few mycologists have realized the true nature of this variability; Klebahn (56, p. 558—560) has suggested alteration of our systematic keys on the basis of certain morphological variations known to occur under conditions of culture. Other mycologists, notably Diedicke

(1) Papers from the Department of Botany of the University of Michigan, no. 245.

(23, p. 2), object to alterations of this kind on the ground that they can not be valid since culture conditions are abnormal and do not occur in nature. Manifestly we have here need of a definition; to pronounce a thing abnormal we must first decide what is "normal" and that is not an easy task. We can not assume the appearance of a fungus as found in the field to be the normal state, because the climatic conditions are too variable even in a single locality, to say nothing of the diversity of conditions affecting a fungus of extensive geographical distribution. By what criterion are we to judge? If we could know all the various environmental factors which affect the morphology of a specific fungus it might be possible to establish a mode and thus arrive at a theoretical normal condition. To be sure, these environmental conditions are difficult to analyze and in reality it is the effect of these conditions, on the morphology of the fruit body, with which we are concerned.

If we regard the host tissues as a source of food for the fungus, is it not conceivable that the same fungus growing on different species of plants, or even upon different parts of the same plant, might vary its morphology in nature just as it would when grown on different artificial media in vitro? Moreover, food is not the only factor to be considered because certainly the moisture, the light, the temperature and the physical character of the substratum are not always the same, even in nature. Evidently we have no means of determining the normal appearance of a fungus. Could we not say that any one of all possible variations induced by environmental factors is a normal condition or aspect? Obviously, then, any condition of the fruit body that we might find in nature would be normal, and similarly any variation induced in culture by alteration or control of environmentals factors could also be considered normal, since variation is merely a normal response of the fungus to a stimulus. After all it would seem that it is not a question of normal or abnormal conditions but rather a question of the extent of the morphological variation occuring in the fruit body of the fungus.

However we are interested at present not only in the extent of variation but also in the possibility of securing a standard basis for differentiation of species and genera. The solution of the problem seems to lie in the use of a standard culture medium with constant conditions of temperature, moisture and light. The combination of this standard method with comparative studies on the morphology of a selected group of fungi ought to reveal fundamental errors in our present scheme of classification. The results in this paper indicate a few of these errors, and point the way for further investigation, but more must be known about connections with the ascomycetes, about morphology, physiology and the existence of biological races among saprophytes before any high degree of stability can be assumed in the group.

This investigation has been done in the Department of Botany of the University of Michigan and was undertaken at the suggestion of Dr. C. H. Kauffman, for whose continued guidance and criticism the writer is deeply grateful.

Historical Review(1).

The development of a scheme of classification in any group of organisms is a gradual and long drawn out process. Many of the genera now classed in the Fungi imperfecti were known quite early. According to Lindau (62) it was Fuckel who originated the term "Fungi imperfecti" and Saccardo in his Sylloge gives Léveillé credit for the term "*Sphaeropsidaceae*". Saccardo's Sylloge was the first attempt to give a definite or extensive classification for the species of the *Sphaeropsidales* and practically all subsequent keys have followed his plan in general, if not in detail.

The more salient characters of organs and structures are ordinarily employed in the artificial keys used to classify plants. In this respect all the keys so far proposed for the *Sphaeropsidales* have had discrepancies due principally to the fact that the morphology of the fruit body has been thoroughly studied for only a comparatively small number of species. Most of the keys are based on quite superficial morphological characters, i. e. principally upon the supposedly mature condition. It is also apparent that some of the discrepancies in the keys are due to wrong interpretations of mature structures because it is possible for two similar structures to have entirely different modes of origin. This is a condition of affairs such as existed in the flowering plants before the morphologists studied the details of structure. Not until the internal structure and development of fruiting bodies is known can any definite system of classification be worked out in the fungi.

Good research along this line has already dealt with scattered single species, but little of it has been done with any particular consideration for standard conditions. Bauke (6) was the first to publish an extensive treatise on the subject and despite the use of liquid media and the presence of contamination he really established some important facts relating to pycnidial origin and the subsequent cavity formation. Brefeld in his "Untersuchungen aus dem Gesamtgebiete der Mykologie" also obtained excellent results but in his case the consideration of the forms within a group was rather secondary since he was endeavoring to prove a certain line of evolution. Klebahn (57) cultured Fungi imperfecti on a large scale but here again the interest was secondary, for he was endeavoring to make connections between perfect and imperfect forms and furthermore he confined himself to a rather narrow group. Others have

(1) For the sake of coherence much of the historical review has been given under the discussion of the various species or genera.

made valuable individual contributions. Ruhland (79) and Fuisting (29) are perhaps the more important of these, although neither of them used culture methods. von Tavel (98) did use culture methods but he restricted himself to a few forms and furthermore attempted too broad generalizations. This last statement applies equally to Voges (101 und 102) who cultured species of *Marssonia* and *Hendersonia* only to find that the pycnidium was not a constant structure in these few species. He then attempted to criticize the entire system of classification in the Fungi imperfecti on that basis. A step in the right direction is the recent work of Kempton (55) on the method of pycnidial origin in a large number of forms and of Dodge (24) on the mode of cavity formation in *Phyllostictina carpogena* Shear, *Sclerotiopsis cancava* (Desm.) Shear & Dodge, and *Schizoparme straminea* Shear.

In the culture of fungi the primary considerations are the physiological relations. It was Pasteur who first developed pure culture methods in bacterial researches and his technique was applied to the study of fungi by various investigators, principally Raulin, Nägeli, Klebs, Brefeld, and de Bary, in the manner indicated by Coons (16) and Bonar (9). Since that time investigators have constantly modified the old and devised new culture media so that a large assortment of synthetic and decoction preparations are now used. Since fungi are very prone to morphological variation under different sets of conditions, it is to be expected that the same fungus grown on dissimilar media may assume different aspects. In fact it is just this very thing that has lead to so much disagreement when one man has tried to duplicate the results of another.

The *Sphaeropsidales* have been rather generally neglected from the standpoint of physiology. The two outstanding papers by Coons (16) and by Leonian (59) have summarized the literature so that there is no need to do so here. The results of these two investigators show that the *Sphaeropsidales* do vary greatly in response to the influence of environmental factors. Indeed the very nature of these variations indicates clearly the need of a standard physiological basis by which we may make morphological comparisons between various types of fruiting structures. According to Coons (16, p. 761) it is commonly admitted that in describing an organism some definite environment must be assumed and that a firm basis for taxonomy can be arrived at, and simplification can come, only from a standardized environment. We must consider, as Kauffman (53, p. 383) has stated, "the question of the constancy of conditions under which these different fungi grew" and that "each species is recognizable, not only by certain prescribed or described characters, but in addition by these characters only when present under certain definite prescribed conditions. . . . . Such a physiological basis for species seems to me the only starting point in a revision of the relationship of the species of any family of plants". Heretofore the main difficulty in culturing large numbers

of species, for comparative purposes, has been the lack of a suitable medium on which one could be certain of obtaining pycnidia. By the use of the medium developed by Leonian (59) this difficulty has been largely obviated.

Methods of Procedure.

During the past four years there have accumulated from various sources a rather large number of pure cultures of *Sphaeropsidales*. These fungi were grown on agar in small loose covered glass dishes (capsules) of about 5 cm diameter and 3 cm height. The medium used was that developed by Leonian (59). The temperature was that of the laboratory and the cultures were placed so as to receive plenty of light. From these cultures there were obtained three sets for embedding in paraffin; 1) young stages for study of pycnidial development and cavity formation; 2) mature stages; 3) stages developed on clover stems laid on the surface of the agar. The last was introduced in order to determine the effect of a more solid substratum. The sectioned material was stained with a combination of Delafield's haematoxylin and anilin safranin. Careful studies were then made of these sections and comparisons made, 1) with the material on the host, 2) with the original descriptions, and 3) with available exsiccati.

Fungi in Culture.

A. Hyalosporae-Hyalodidymae (Sensu Saccardo).

Phoma betae Franck. Tissue isolation by Lee Bonar from Michigan sugar beets. 1922.

Phoma astragali Cooke & Harkn. On *Aragalus* sp., Nelson's Ranch, Wyoming, July 24, 1922. Collected by L. E. Wehmeyer.

Diplodina coloradensis E. & E. On dead stems of *Senecio* sp. Brooklyn Lake, Wyoming, July 24, 1922. On dead stems of *Aster proximus* Greene Medicine Bow National Forest, Wyoming, July 29, 1922. Collected by L. E. Wehmeyer.

Ascochyta meliloti (Trel.) Davis. On dying stems of *Melilotus alba* Desr., Ann Arbor, Mich., October 7, 1923. W. A. Archer (no. 75).

Phyllosticta cacti (Berk.) Archer. On *Opuntia arborescens* Engelm., State College, N. M., January, 1920. Collected by L. H. Leonian.

Septoria lycopersici Speg. Subculture from stock culture in the laboratory.

Phomopsis arctii (Lasch.) Trav. On dead stalks of *Arctium* sp., Ann Arbor, Mich., April 30, 1923. W. A. Archer (no. 51).

Phomopsis coneglanensis (Sacc.) Trav. On branches of *Aesculus hippocastanum* L., Ann Arbor, Mich., December 8, 1922. W. A. Archer (no. 45).

Cytospora minuta Thüm. On branches of *Fraxinus americana* L., Belleville, W. Va., December 27, 1921. Collected by Lee Bonar.

Cytophoma pruinosa (Fr.) v. H. On branches of *Fraxinus* sp., Ann Arbor, Mich., March 16, 1922. W. A. Archer (no. 14).

B. Phaeosporae-Phaeodidymae (Sensu Saccardo).

Sphaeropsis conspersa (Schw.) comb. nov. On branches of *Robinia pseudo-acacia* L., Ann Arbor, Mich., January, 1922. W. A. Archer (no. 10).

Sphaeropsis hyalina (B. & C.) Archer. On *Fraxinus americana* L., Belleville, W. Va., December 27, 1922. Collected by Lee Bonar.

Sphaeropsis propullans (Schw.) Peck. On *Celastrus scandens* L., Ann Arbor, Mich., December, 1923. W. A. Archer (no. 22).

Sphaeropsis glandulosa Cooke. On *Ailanthus glandulosa* Desf., Ann Arbor, Mich., January, 1922. W. A. Archer (no. 26).

Sphaeropsis sumachi (Schw.) Cke. et Ell. On branches of *Rhus glabra* L., Ann Arbor, Mich., March 16, 1922. W. A. Archer (no. 46).

Sphaeropsis gallae (Schw.) Archer.

Dothiorella gallae (Schw.) Starb. On old fallen oak galls, Whitemore Lake, Mich., September 29, 1923. W. A. Archer (no. 72).

Dothiorella glandicola (Schw.) Starb. On fallen acorns, Ann Arbor, Mich., January, 1922. W. A. Archer (no. 27).

Dothiorella quercina (C. & E.) Sacc. On bark of *Quercus* sp., Ann Arbor, Mich., April, 1922. W. A. Archer (no. 43).

Botryodiplodia ostiolata E. & E. On bark of *Quercus rubra* L., Ann Arbor, Mich., October 25, 1921. W. A. Archer (no. 9).

Sphaeropsis visci (West.) Archer. On leaves of *Phoradendron* sp., State College, New Mex., December, 1921. Isolated by L. H. Leonian from a commercial shipment of mistletoe.

Camarosporium robiniae (West.) Sacc. Growing in old fruit bodies of some fungus. On bark of *Robinia pseudo-acacia* L., Ann Arbor, Mich., January, 1922. W. A. Archer (no. 19).

Hendersonia rubi (West.) Sacc. On dead canes of *Rubus* sp., Ann Arbor, Mich., May 15, 1922. W. A. Archer (no. 55).

Coniothyrium concentricum (Desm.) Sacc. On leaves of *Yucca macrocarpa* Englem., State College, New Mex., January, 1920. Collected by L. H. Leonian.

C. Pachystromaceae sphaeriales, Erectae-Coriaceae (Sensu von Höhnel).

Micropera caespitosa (Peck) Archer. On branches of *Ilex verticillata* (L.) Gray. Ypsilanti, Mich., April 21, 1923. Collected by L. E. Wehmeyer.

Micropera drupacearum Lév. On branches of *Prunus* sp., Ann Arbor, Mich., December, 1923. W. A. Archer (no. 74).

Micropera spuria (Fr.) v. H. On branches of *Prunus americana* Marsh., Ann Arbor, Mich., June, 1921. W. A. Archer (no. 59).

Naemosphaeria acerina (Peck) v. H. On *Acer rubrum* L., Ann Arbor., Mich., January, 1922. W. A. Archer (no. 31).

D. Melanconiaceae (Sensu Saccardo).

Pestalozzia guepini Desm. Culture furnished by Dr. C. D. La Rue, University of Michigan.

Pestalozzia palmarum Cooke. On young fallen fruits of *Cocos nucifera*, Ft. Myers, Fla., August 28, 1923. Collected by L. E. Wehmeyer.

Vermicularia circinans Berk. On bulbs of *Allium cepa* L., Ann Arbor markets, October, 1920. Collected by L. H. Leonian.

Vermicularia peckii Sacc. On dead stems of *Trillium declinatum* (Gray) Gleason. Ann Arbor, Mich., May 19, 1923. W. A. Archer (no. 49).

Developmental morphology.

A. Hyalosporae-Hyalodidymae.

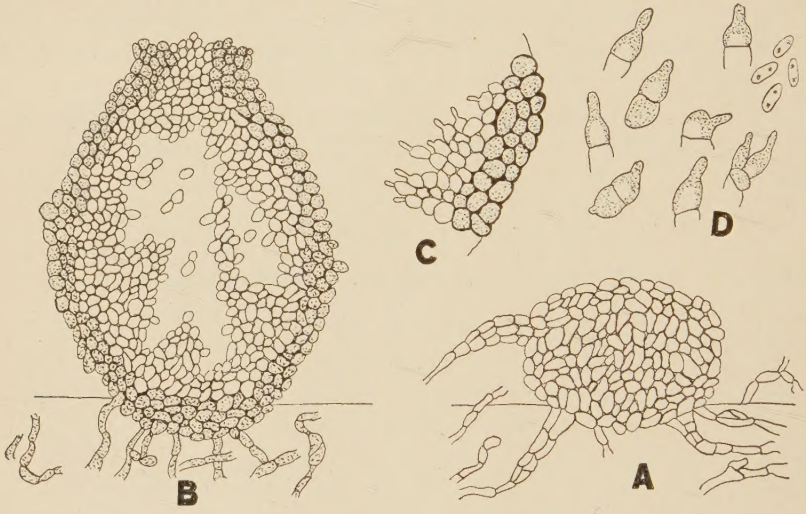
Phoma betae Franck.

Cultural characters. The middle stratum (1) is dark brown at the center shading to a lighter brown, with a tinge of green toward the margins; the aerial stratum consists of short fuzzy, white to grayish hyphae; while the submerged stratum consists of brownish strands. The pycnidia are numerous on agar but in agar with layered clover stems they are confined mostly to the stems.

Paraffin sections. The globose primordia form superficially on the agar (text fig. 1, A) or below the cuticle when arising on the clover stems. They evidently form endogenously, sometimes two or three hyphae being involved, and consist of hyaline, small-celled pseudoparenchymatous tissue. When they have attained a size of 200—400 μ the outer layers have become differentiated into swollen, thick-walled brown cells thus forming an enveloping outer wall. The papillate ostiole is formed by the outward growth of the inner hyaline cells, which ruptures the brown enveloping layer (text fig. 1, B). The cavities arise at several points as a result of the dissolving or gelatinizing of a few cells, the spores then form by budding directly from the primordial cells surrounding the cavities (text

(1) In the agar cultures all the fungi regularly formed three strata of hyphae; an aerial, a middle and a submerged layer. The middle stratum appeared far more constantly than the other two. It developed just at the surface of the agar and consisted of a more or less dense mat of vegetative hyphae. In the cultures of most species this stratum became brown or black.

fig. 1, C). There does not seem to be much regularity in the development of the cavity since the spores may continue to arise at various points, much as described for *Asterosporium hoffmanni* (3). In nearly mature pycnidia the spores are tightly packed in the irregular cavity and one often finds isolated bits of primordial tissue surrounded by the spore mass. The method of spore formation is like that given by Bauke (6) for the pycnidial form of *Curcurbitaria elongata* and by Brefeld (10, p. 124, pl. 10, fig. 3—4) for *Pycnis sclerotivora* Bref. but the exact process is only indistinctly determined from sectioned material because of the minuteness and abundance of the spores and also on account of the presence of a



Text fig. 1. *Phoma betae.*

A Young primordium on agar. B Mature pycnidium on agar, with dark outer layer and hyaline tissue within. C Portion of pycnidium in B, enlarged to show mode of spore formation. D Detail of spore formation. On the spore mother cell there forms a protuberance which grows gradually larger and then becomes detached to appear like the spores represented in the upper right corner.

gelatinous substance which renders staining difficult. However if one crushes out very young pycnidia from fresh cultures at the primary stages of spore formation it is quite evident that the spores arise by direct "budding" from the primordial cells (text fig. 1, D) and in such material it is possible to distinguish all stages of development. Evidently by the mere pushing out of the flexible cell wall a minute protuberance arises which grows gradually larger at the expense of the cytoplasmic contents of the cell. In fact at an early stage there appears near the lower end of the parent cell a small vacuole which grows correspondingly larger as the spore increases in volume, whereby one is reminded of the similar process illustrated by Higgins (38, p. 439, text fig. 2, f—g). To all appearances the vacuole serves to force the cytoplasm into the spore.

Phoma astragali Cooke & Hark.

On the host. The original description of *Phoma astragali* is so brief that there can be no certainty that the fungus at hand is the same species. In the writer's collection the pycnidia are evenly distributed, broadly globose and tardily erumpent through the epidermis; the ostiole is small and pore-like. The spores are rather irregular in size, fusoid to oblong-cylindrical, hyaline, 5—10 ⩻ 2—5 μ. No conidiophores were observed.

Cultural characters. The middle stratum is medium thick and blackish; the aerial, grayish, fuzzy and wilted into irregular clumps; the submerged, delicate, hyaline, with ramifying hyphae. The surface of the colony is convoluted into several radiating ridges which mark off the several sectors. In some of these sectors the pycnidia, after eight days, form so thickly as to blacken the entire area, while in other sectors they are few and scattered. On clover stems the pycnidia do not form so readily. Some of the pycnidia form normal spores, i. e. the same shape and size as on the original substratum, while others form a small rod-shaped type, measuring 2 ⩻ 1 μ. The spores exude in moist droplets.

Paraffin sections. The development is very similar to that described for *Phoma betae.*

Diplodina coloradensis E. & E.

On the host. The pycnidia are evenly distributed, black, globose, distinctly ostiolate, 100—300 μ diameter, arise in the outer part of the cortex and finally appear to be entirely superficial. The wall is 10—20 μ thick, composed of several layers of brown, isodiametrical, large, thick-walled cells. The spores arise from the entire surface of the cavity on almost invisible conidiophores. The spores in smaller, young pycnidia are cylindrical to sometimes narrowly elliptical, 5—12 ⩻ 2—3 μ, 1-celled and 2-guttulate, but in larger, mature pycnidia are 17—20 ⩻ 3—4,5 μ, 2-celled, hyaline and greenish-tinged. Associated with an immature *Didymella?*

Cultural characters. The middle stratum is tawny to dark brown. The aerial stratum forms a smooth overlying mat which is white at the center, merging to a smoky gray at the margins. The medium is discolored a dark smoky-brown. The pycnidia are rather sparse and on agar are covered by the aerial mat.

Paraffin sections. The pseudoparenchymatous primordia arise just below the epidermis of the clover stems, but finally become erumpent. The cavity arises at the center without any apparent accompanying gelatinization of the primordial tissues. The cells surrounding the cavity do *not* divide to form a rim of small cells below the hymenium as in *Sphaeropsis* but instead the spores arise directly from the peripheral and unchanged primordial cells. When nearly mature the pycnidia are tightly packed with a solid mass of spores and shortly afterward the ostiole for-

mation ensues, being preceded by the proliferation of an apical mass of buffer tissue. The pycnidia in culture usually measure 100—250 μ but quite often may be smaller; younger pycnidia often form in or on the mature ones. In the sectioned paraffin material the pycnidium of this fungus bears a close morphological resemblance to those of *Phoma*, *Phyllosticta* and *Ascochyta*.

Comments on the genera Phoma and Diplodina. Shear (83) has set forth quite plainly the confusion that exists among the numerous species of the genus *Phoma*, while Grove (32) and von Höhnel (48, p. 98—100; 46, p. 237; etc.) have attempted to clear up this confusion, the former by indicating the synonomy and the latter by making several new genera. Of these new genera, *Sclerophomella*, *Sclerochaeta*, *Botryophoma* and *Sclerophoma*, classed as "Sclerophomaceen", appear under the division of *Endogenosporae* (50, p. 306). The latter group von Höhnel characterizes partially as follows; "Conidien im Innern der hyalinen Zellen einzeln oder zu mehreren gebildet, durch schleimige Histolyse der Zellen freiwerdend, einzellig oder quergestellt, meist hyalin oder blaß, seltener braun." This describes a process of spore formation by cleavage within a primordial cell and the spores would therefore correspond to similar cases in the fungi where they are known to be of endogenous origin.

By the usual method of examining ordinary herbarium material of species of *Phoma*, including the two described in this paper, the mode of spore formation can not be determined accurately, due principally to the extreme smallness of the pycnidia and the spores. However, in the accounts just given by the writer it was shown that in material from cultures the spores arise by budding from the cells and not endogenously in the sense of von Höhnel. Van Luyk (63, p. 133) made repeated examinations of *Sclerophoma pityophila* (Cda.) v. H. and found no trace of endogenous spore origin but on the contrary only budding from the cells. Petrak (75, p. 87) has discussed at length this new group of "Sclerophomaceen" in so far as it has to do which spore origin and, from his examination of herbarium material, has decided that in many of von Höhnel's genera the spores are not endogenous but rather are borne directly on the walls of the inner pycnidial cells. Petrak does, however, retain the conception of endogenous spore origin for at least three of the five tentative groups which he himself made. Group II of this tentative arrangement is founded on the species *Sclerophoma pityophila* which van Luyk (l. c.) claims does not have endogenous spores. *Sarcophoma miribelii* (Fr.) v. H., representative of Group III, has been examined by the writer in the exsiccati (*Macrophoma miribelii* (Fr.) Berl. & Vogl. in Sydow Myc. germ. no. 617) and there is no evidence of spores arising endogenously. Pycnidia crushed out under a coverslip and carefully examined, with oil immersion, show that the spores arise directly from the cell walls. Furthermore the spores have a distinct scar on the lower end

indicating the point of attachment. Such scars are common enough in many of the larger spores of other genera in the *Sphaeropsidales* and it would seem that this one fact alone would militate against the theory of endogenous origin of spores in this as well as a number of other species. Meanwhile Petrak has reaffirmed von Höhnel's statement that such a process occurs, but finds it in only a portion of the forms reported by von Höhnel.

Considering that most of the species of the Endogenosporae have been drawn from the genus *Phoma* it is to be regretted that the genera can not be retained in their original form as erected by von Höhnel. Although it is not well to generalize from too few examples yet it is quite evident that the genera of the Endogenosporae are founded, in part at least, on incorrect characters. A careful examination of *Sclerophoma (Dothiorella) concaviuscula* (E. & B.) v. H., in Ellis & Ev. N. Amer. Fungi no. 3546, and *Dothichiza (Dothiorella) minor* (E. & E.) v. H., in Ellis & Ev. N. Amer. Fungi no. 3356, proves that neither belongs to the Endogenosporae but that both bear spores directly on the cell walls.

The facts given for *Diplodina coloradensis* would imply that the younger pycnidia with their 1-celled spores could easily pass for the *Phoma senecionis* Syd. as described in Saccardo's Sylloge. Furthermore Kauffman (54, p. 201) reports that *Diplodina citrullina* Grossenb. in a certain environment produces 1-celled spores which seem to be merely an arrested condition of the 2-celled state. There is no reason against assuming that these particular conditions could exist also in nature and it seems most likely that many of the species of *Phoma*, especially those reported with two oil droplets in the spores, are in reality just such cases of arrested development and under proper conditions would produce 2-celled spores.

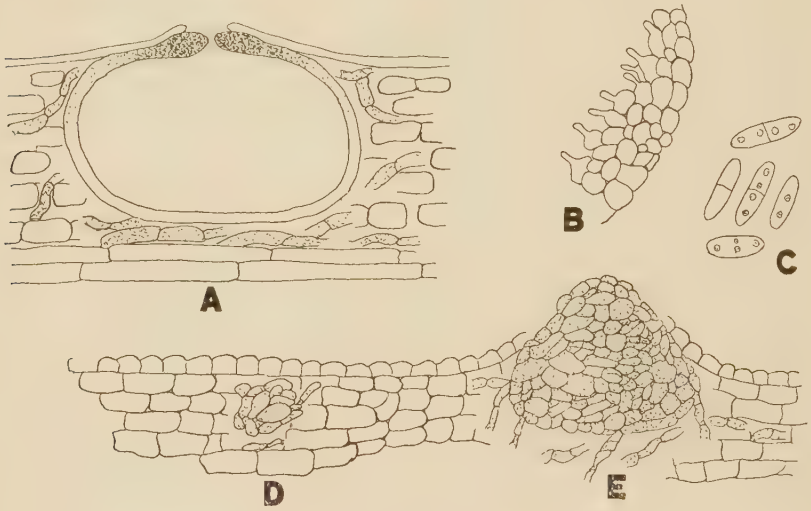
With such existing confusion there can be no immediate hope of solving systematic problems in this group until much careful cultural and cytological work is done. As Petrak (75, p. 103—4) has aptly stated: "Erst wenn alle bisher als *Phoma*, *Phyllosticta* usw. beschriebenen Pilze genau untersucht sein werden, wird es sich zeigen, auf wie viele verschiedene Gattungen diese zahllosen Formen zu verteilen sein ....."

Ascochyta meliloti (Trel.) Davis.

On the host. The pycnidia occur as minute dot like structures scattered on the stems and when young have a yellowish hue but later become almost black. Hand sections show that the fruit bodies arise just below the cuticle and remain covered by it (text fig. 2, A). The wall measures about 10 μ in thickness and consists of brown parenchyma cells usually paler or even hyaline toward the base of the pycnidium but quite often uniformly brown. The spores are not borne on conidiophores but arise directly from the peripheral cells (text fig. 2, B) and are mostly 1-septate; in many pycnidia, however, they are non-septate, this condition, no doubt,

being a younger stage (text fig. 2, C). The ostiole is a mere pore in the upper wall.

Cultural characters. Usually the mycelial growth is medium brown in color with no aerial hyphae. However some of the cultures become almost black and a microscopic examination shows that nearly all the mycelium has been converted into heavy walled chlamydospores. Usually in such cultures no pycnidia are formed or at least only sparingly, as reported by Stone (94, p. 583). Ordinarily the pycnidia arise in rows which radiate from the center of the culture surface.



Text fig. 2. *Ascochyta meliloti.*
A Mature pycnidium on host, remaining covered by cuticle. B Detailed portion of pycnidium in A, to show nature of tissue and mode of spore origin. C Types of spore obtained from mature pycnidium. D Early stages in formation of primordium in clover stem in culture. E Older stage of primordium.

Paraffin sections. On clover stems the primordia form below the cuticle but gradually become erumpent as they increase in size (text fig. 2, D—E). On agar the pycnidia are inclined to become globose and superficial. The spore cavity arises near the center of the primordium, enlarges until is has used up nearly all of the tissue and finally leaves only a thin surrounding rim composed uniformly of brown parenchyma cells. The same pore-like ostiole described above for forms grown on the host was observed in the cultures, but was somewhat more prominent and wider. In general the fruit bodies resemble those already described for *Diplodina coloradensis* (p. 9).

General remarks on the genus. The genus *Ascochyta* originally contained the species which were leaf parasites but Allescher (1, p. 624—5) distinguished between this genus and *Diplodina* by confining to the latter

those species growing on stems. This was, of course, a highly artificial separation and was found to be unsatisfactory in cases where the same species was known to occur on both stems and leaves. Diedicke (21, p. 138 and 23, p. 369) realized this discrepancy and proceeded to establish other characters for distinguishing the two genera, i. e. the characteristics of the pycnidial wall. He states, for *Ascochyta* (21, p. 139): "Von einer wirklichen Wand ist im unteren Teile des Gehäuses nichts zu bemerken. Das hyaline, interzellular wachsende Myzel des Pilzes tritt einfach etwas dichter zusammen, die gewundenen Hyphen legen sich etwas aneinander und bilden auf diese Weise ein hyalines, lockeres, dem Fruchtlager der Melanconieen ähnliches Geflecht, von dessen innerer Seite die Sporen abgesondert werden. Nur nach oben bildet sich durch noch dichteres Zusammenwachsen, sowie durch Bräunung der Fäden eine echte Wand aus, die man als parenchymatisch bezeichnen kann." And for *Diplodina* (21, p. 140) he says: "Gehäuse vollständig, ringsum parenchymatisch, aus dünnwandigen Zellen bestehend, mit ein- oder mehrschichtiger Wand." Diedicke's interpretation of pseudopycnidium in *Ascochyta* is based on the text figure for *Septoria podagrariae* Lasch given by Potebnia (78, p. 65, fig. 15) but if one considers the definition of the structure given by Potebnia (l. c., p. 69—70) in comparison with the facts presented in this paper it clearly is seen that the fruit body of *Ascochyta* is not a pseudopycnidium. Diedicke states (21, p. 139) that the pycnidial wall in *Ascochyta* species is always brown above and hyaline below, even when stem-inhabiting. The writer wishes to disagree pointedly with this statement. An examination of *Ascochyta caulicola* Laub., Syd. Myc. germ. no. 37, given as a synonym of *A. meliloti* (Trel.) Davis (18, p. 663) and listed by Diedicke (21, p. 139) as typical of the genus, reveals mostly depressed pycnidia, — only a few are globose — and while the wall is usually brown above and hyaline below, yet a few pycnidia were found in which the entire wall was uniformly brown. It has been indicated already that although *A. meliloti* on its natural host has pycnidia with hyaline or subhyaline basal walls, yet when formed on agar the pycnidia have uniformly brown walls throughout. An especially good example is the often named but evidently little studied *Ascochyta chenopodii* (Karst.) Died. as represented in Sydow Myc. germ. no. 2185. This fungus, growing on leaves, has a pycnidium with a distinct wall which is brown throughout its entire circuit, yet Diedicke (23, p. 373) states thet the fruit body has a pseudopycnidial structure. *Ascochyta pteridis* Bres., Sydow Myc. germ. no. 2186, listed by Diedicke as typical of the genus, also has walls which are distinctly brown throughout.

It is to be admitted that many of the Ascochytas do have pycnidia with hyaline basal walls and that the Diplodinas have uniformly brown walls but since the former are generally leaf parasites and the latter stem saprophytes it would seem that the cause for this difference is to be

found in the immediate environment of the respective host tissues. The situation is like that existing for *Coryneum* and *Hendersonia* on *Rubus* (p. 48). If then this pseudopycnidial character is set aside there can no longer be any valid reason for retaining the distinction between the genera *Ascochyta* and *Diplodina*(1). This would apply also to the other genera of the Hyalodidymae where Diedicke (23, p. 372) used the term of "pseudopycnidium" in key separations.

Phyllosticta cacti (Berk.) comb. nov.

Phoma cacti Berk.
Phyllosticta opuntiae Sacc. & Speg. var. *microspora* Cav.
Phyllosticta opuntiicola Bubák
Phyllosticta concava Seaver (81, p. 13).

On the host. Irregular grayish sunken spots with elevated margins occur on various parts of the plant. The pycnidia are blackish, globose, rather thickly scattered in the spots and measure about 100—200 μ diameter. They are borne just below the cuticle, with the pore-like ostiole protruding and in older fruit bodies the overlying cuticle is blackened. Surrounding the ostiole there are often seen a few short brown setae which protrude through the opening in the cuticle. It seems quite possible that these function in rupturing the thick cuticle because in some of the younger pycnidia they were seen penetrating the still unruptured cuticle. The pycnidial walls are composed of brown parenchyma tissue, the outer layers being much darker. The spores arise directly from the more hyaline cells lining the cavity, are rod-shaped, straight, 1-celled, hyaline, measure 3—5 ⩒ 1—2 μ (mostly 3—4 ⩒ 1,5 μ) and have rounded ends. Some are biguttulate and a few are slightly curved.

Vertical sections through the diseased portion of the host indicate that the mycelial development is mostly deep in the chlorenchyma tissue and that columns of hyphae arising in the substomatal cavities push upward to form finally the pycnidia just below the cuticle in the epidermal layer. This is much like the process given by Wolf (109) for *Perisporium mendozanum* Speg. (109, fig. 5) and *Gloeosporium lunatum* E. & E. (109, fig. 20).

Cultural characters. The middle stratum is at first colorless, changing to dirty white; the aerial scanty. The medium is rendered opaque by fine ramifying hyphae. The surface is smooth, moist, cream colored, sometimes with brown patches. The pycnidia appear in media only after five months and then only on the drier portions. On the clover stems they are plentiful after seven weeks. The spores are more variable than on the host, measuring 2—4 ⩒ 1—2 μ and most of them are ovoid.

(1) This agrees with the recently found statement made by Petrak in Annal. Mycol. 23: 43.

Paraffin sections. In development and appearance the pycnidia are quite like those described under *Phoma*, *Ascochyta* and *Diplodia*. The setae described in forms from the host do not develop in culture.

Synonomy of species. The descriptions of the species of *Phyllosticta* on *Opuntia* as compiled in Saccardo's Sylloge all overlap to a surprising degree and evidently there is no distinction except in spore size. Even this, in most cases, would not be a barrier to reducing the various species to synonomy but since the spores of the fungus in culture have remained constantly below 5 μ in length it seems necessary, for the present at least, to consider them under two species as follows:

Phyllosticta opuntiae Sacc. & Speg. (Spores 5—8 ⩽ 3—4 μ)

Syn. *Phoma cacti* Berk. var. *opuntiae* Sacc.

Phyllosticta cacti (Berk.) Archer (Spores 3—5 ⩽ 1—2 μ).

The short, filiform conidiophores reported in the original descriptions of several of the above species were, quite likely, merely the attached spores as shown in text fig. 1, C for *Phoma betae* and in text fig. 2, B for *Ascochyta meliloti*.

Septoria lycopersici Speg.

The morphology of this fungus, both on the host and in culture, has been thoroughly presented by Levin (61) but studies of the present material indicate that certain facts concerning cavity formation were overlooked or at least not mentioned. It is important that this point be cleared up since there seems to be some misunderstanding in the literature regarding the fruiting structure of species of *Septoria*. The primordium appears at the intersection of a few hyphae. The resulting clump of cells increases in diameter and as Levin (l. c. p. 26) says: "consists of a hollow, globose body, without an ostiole, with a few strands of mycelium crossing the cavity within". In the material studied by the writer it was observed that these hyphae undergo dissolution to form a dense, vacuolated, gelatinous substance which fills the cavity (Pl. 1, fig. 2—3); later the spores arise from the periphery of the cavity, push into this substance and subsequently displace it altogether.

The wall in superficial pycnidia is composed of three to seven rows of brown, thick-walled, parenchyma cells (Pl. 1, fig. 2). There is evidently some connection between exposure to air and this browning of the tissues because in those pycnidia which are entirely or partially immersed in the substratum the browning does not occur at the base (Pl. 1, fig. 1) and it is common to find examples of fruiting structures, formed more deeply within the agar, in which all traces of primordial tissue have disappeared; leaving merely a naked pocket of spores. The writer believes that this browning of the tissues is an important factor in the formation of the pycnidial wall. When browning ensues this portion of the tissue is no longer readily available for the production of spores,

instead it remains unchanged, so that it is ordinarily recognized as the pycnidial wall. Levin (l. c. p. 28) has explained the formation of the typical "wide ostiole" by indicating that the enlarging mass of spores exerts a gradually increasing force and suddenly breaks through this three- to five-celled wall at the point of least resistence. This weak place in some pycnidia would be, of course, the basal unbrowned tissue. The writer's examination of ostiole formation leads him to believe that there is another important factor concerned, i. e. a dissolving action. The evidence for this is based on the presence of brown, thick-walled primordial cells lying free within, or else lining the cavity which give every appearance of having been partially dissolved. It is a well known fact in other fungi that cortical cells of the substratum are often dissolved by fungous hyphae and there is reason to assume that the same process applies within the pycnidium. The combination, then, of this dissolving action on the wall together with the internal force of the spore mass would certainly explain the wide and irregular "ostiole" common to species of *Septoria*.

Levin (l. c. p. 28) is inclined to accept the definition, given by Diedicke (22, p. 484), for the fruiting structures in the genus *Septoria*. The definition reads as follows: "*Septoria* umfaßt alle diejenigen Arten, deren Fruchtlager sich durch Ausbildung einer Decke in ein pseudopyknidiales Gehäuse umwandelt, das oben mehr oder weniger breit geöffnet ist." While *Rhabdospora* (23, p. 523) is differentiated from *Septoria* by . . . "ringsum geschlossen und von parenchymatischem Gewebe, meist mit einem Porus versehen". This conception of a "pseudopycnidium" was first employed by Potebnia (78) in connection with the fruiting structure of certain species of fungi. There may be some justification for the term. The writer is not prepared to deny the existence of such a structure, but a study of the facts presented by Potebnia will indicate several weak points. The writer believes that inadequate attention was originally given to young developmental stages of the fruiting structures and that wrong interpretations were placed on several of the figures. To begin with, Potebnia (l. c. p. 65) in speaking of *Septoria podagrariae* Lasch states: ". . . . ihre Fruchtgehäuse nicht wie echte Pykniden gebaut sind. Die meist zarte Wand der Fruchtkörper besteht nur aus einem Gewebe von Hyphen, welches den Hohlraum, der in dem Blattgewebe durch die zerstörende Tätigkeit des Pilzes entstanden ist, umgibt. Solche Fruchtgehäuse nenne ich Pseudopykniden." His figure 15 illustrating this point is not so different from that of *Septoria lycopersici* given in this paper. Farther on, Potebnia (l. c. p. 69), speaking of *Septoria piricola* Desm., modifies this first definition by the following: ". . . . habe ich eine Abbildung des oben beschriebenen Fruchtkörpers entworfen (fig. 20), aus welcher ersichtlich ist, daß das Gehäuse nicht wie bei den echten Pykniden aus pseudoparenchymatischem (paraplektenchymatischem) Gewebe, sondern

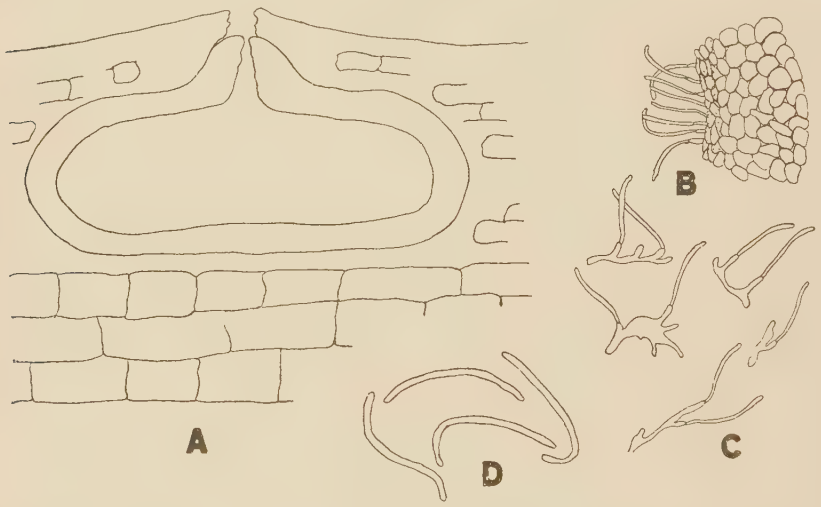
nur aus miteinander verflochtenen Hyphen (einem Prosoplektenchym) besteht, wodurch meine Annahme, daß die *Septoria*-Fruchtkörper keine echten Pykniden darstellen, sondern Pseudopykniden sind, deren Gehäuse durch die Bildung von Hyphen um die Sporenlager entstehen, bestätigt wird. Die Hyphen wachsen von der Basis nach der Mündung zu, wodurch sich die verschieden große Öffnung der Gehäuse erklärt." The writer considers there has not been a single fact presented to prove that the pycnidial wall does form in this way or that the fruiting body of *Septoria* is any more "pseudopycnidial" than those of *Sphaeropsis* or *Phoma* species.

There is still another point to be considered, i. e., that of the hyaline appearance of the pycnidial wall in many of the Septorias as they occur in the host tissues. It is this hyaline appearance of the pycnidial wall which has led Diedicke and others to accept the "pseudopycnidial" idea. Judging, however, from the facts already presented for *Septoria lycopersici* and to be shown for *Hendersonia rubi* it might be suggested that the hyaline nature of the wall is not inherent, and therefore not a good distinguishing character. The wall is hyaline merely because the factors or conditions necessary for the browning process are absent and some Septorias do have brown walls even on the host, as in the case of *Septoria gladioli* Passer, reported by Massey (64, p. 158). On many plants with a species of *Rhabdospora* (brown-walled, following Diedicke) on the stems, there can be found also a *Septoria* (with hyaline wall) on the leaves, yet in all other respects the two species correspond. This is evidently a parallel to the facts given under *Hendersonia rubi* (p. 48) and obviously the explanation presented there applies here.

Phomopsis arctii (Lasch) Trav.

On the host. From above, the pycnidia are seen to be covered by minute blackened spots through the center of which projects the scarcely visible ostiole. Hand sections show that the pycnidia are entirely embedded in the thin cortex and that the blackened spots are in reality due to the discoloration of the surrounding tissues, especially in those portions above the pycnidium. The pycnidia (250 μ diam.) are globose to slightly depressed, with the flattened base seated on the wood tissues; the papillate ostiole is rather blunt and thickened. The wall tissue is thin, composed of minute and brown parenchymatous cells and definitely blackened and thickened only at the top (text fig. 3, A). The cavity is lined by short rod-shaped conidiophores (text fig. 3, B) bearing thread-like, straight or curved, hyaline spores (text fig. 3, C—D). No fusoid spores, of the other type common to *Phomopsis*, were found. This was evidently a collection of the young stages of development because many primordia were found in which no cavity had formed, there being only a mass of hyphae with the characteristic discoloration of the host tissues.

Cultural characters. The middle stratum is light brown, changing to black; aerial, scanty and white, later dense-fluffy. The culture was obtained by the ready germination of the filiform spores. Pycnidia were formed. At first only the filiform spores were found in culture but later (after a month or so) the fusoid type made its appearance to the practical exclusion of the first kind. On both agar and stems the pycnidia are immersed, thereby making it difficult to detect their presence except by sections or by teasing out portions of the colony. The germination of the filiform spores in this case is of great interest, because it is rarely that anyone succeeds in germinating these spores and it has even been suggested that they are not genuine spores.



Text fig. 3. *Phomopsis arctii.*
A Diagram of pycnidium embedded in cortical tissue of host. B Detailed portion of pycnidial wall from A. C Types of conidiophores obtained by crushing out pycnidia. D Various types of filiform spores. (Vide Plate 3.)

Paraffin sections. The primordia in agar occur in crowded numbers, immersed below the surface at various levels. The smaller ones measure 5—15 μ diameter. Their origin seems to be chiefly symphogenetic and as they increase in size they are seen to be composed of a prosenchymatous tissue, the cells being brown and quite irregular as to shape and size. The cavity in the first stages of formation is not so distinct or crescent-shaped as in *Phomopsis coneglanensis* but in mature fruit bodies the cavity is rather irregular in outline, corresponding more or less to the shape of the primordium. Those pycnidia arising near the surface of the agar, when mature, are globose, with a papillate ostiole and with a browned outer layer, but those forming deeper are quite different. None of the latter develops the papillate ostiole, nor is there a distinct

outer wall. Instead the behavior is more like that described for the pycnidia of *Septoria lycopersici* (p. 15). When the cavity reaches maturity, in the partially or totally embedded pycnidia, a varying length of the pycnidial wall is dissolved away leaving an opening into the agar; often in fact, the entire wall is dissolved away leaving nothing but a naked pocket of spores in the agar. This again is an example of the part played by the brown, enveloping outer layer in the formation of the pycnidium. Diedicke (20, p. 10) in discussing the pycnidial wall of *Phomopsis* says: "Je weiter nach oben zu, und vor allem je weiter die Epidermis durchbrochen wird und das Gehäuse an die Luft oder ans Licht tritt, desto dichter wird dieses Gewebe, desto mehr färben sich seine Elemente ...."

On clover stems the primordia arise in the cortex and as they increase in size they break apart and disintegrate the cortical tissues. Sometimes they arise in clusters (Pl. 2, fig. 1) and then become confluent at an early stage to form a compound primordium which functions in the same manner as a simple primordium but which forms a correspondingly larger pycnidium (Pl. 2, fig. 2). Cavity formation arises by the dissolution of a few central cells and then the surrounding cells undergo division to form a layer of small, elongated cells from which the conidiophores arise. When nearly mature the pycnidia are partially erumpent and usually have an irregular cavity. The ostiole arises as the result of an elongation or proliferation of apical tissue in the pycnidium. In old cultures (9 months) this elongation continues, finally resulting in a cylindrical beak several times longer than the pycnidium proper, taking on, in a deceptive manner, the form of a beaked pycnidium of another genus.

Examination of exsiccati. A study of the specimens of Sydow, Myc. germ. no. 1013, shows that the fusoid spores are contained in the larger and older pycnidia while the filiform type is found in the smaller and evidently younger pycnidia, some of which had not yet formed an ostiole. The mature pycnidium (500 μ diameter) has a thick brown wall (45—60 μ) which is composed of a definite outer layer of large irregular cells, with intermixed cortical tissue, and an inner layer consisting of small, more regular cells. In the young pycnidia the walls are thinner (15—25 μ) and lighter colored; consisting mostly of meristematic tissue, i. e. the entire layer is concerned with the formation of the conidiophores. It is quite evident that the young pycnidia increase in size by the accretion of new tissue formed from the proliferation of the outer layers of the pycnidium and perhaps also from ramifying hyphae that have previously penetrated and discolored the host tissues. This would explain the presence of the intermixed cortical cells as seen also in the pycnidia formed in culture on the clover stems. Diedicke (20, p. 9—10) has described the exact nature of these surrounding ramifying hyphae. Many of the younger pycnidia contained straight spores, while in others the spores were typically curved. Diedicke (l. c. p. 15) reports, in the case of

Phomopsis casuarinae, that the straight spores are a younger stage of the curved ones. Bresadola (14) reported two species of *Rhabdospora* on *Lappa officinalis*. They differed only in that *R. lappae* Feurich had straight spores while *R. lusatica* Feurich had curved ones. Petrak (70, p. 210) considers *R. lappae* to be a form of *Phomopsis arctii* but he fails to take into account *R. lusatica*. From the facts presented in the preceding paragraphs it is evident that this species also should be a synonym of *Phomopsis arctii*.

Phomopsis coneglanensis Trav.

On the host. The pycnidia arise in the cortex just below the periderm and have an approximate diameter of 500—600 μ. The tissue is composed of hyaline, irregular cells, i. e. pseudoprosenchyma. The crescent-shaped cavity is lined all around by conidiophores and develops in such a manner as to leave a mound-shaped projection of tissue at the base of the pycnidium. After spore formation has proceeded for some time there ensue the processes which result in the rupture of the overlying periderm and the subsequent formation of an ostiole. Evidently the rupture of the periderm is brought about by the elongation and growth of all the cells along the upper part of the pycnidium. The tissue thus formed consists of more or less parallel rows of oblong cells. The ostiole then forms in a papillate growth of tissue arising evidently from an inner layer of cells. Observations of pycnidial development on clover stems, however, indicate that the epidermis was perforated by the papillate ostiole which formed first and that the elongation of the upper peripheral cells then completed the rupture and upheaval. Here and there throughout the wall tissues of the pycnidium there can be found disintegrated portions of cortical tissue. The spores measure 7,5—10 ⩽ 2—3,5 μ.

Cultural characters. The middle stratum is white and thick, later becoming brownish; aerial, felt-like, white and matted. The medium is rendered opaque by ramifying mycelium. Pycnidia on the agar are partially submerged and tend to form concentrically. They mature more quickly on the clover stems. Both types of spores are formed, the filiform ones being 15 ⩽ 1 μ.

Paraffin sections. The primordia in agar cultures are globose, pseudoprosenchymatous, and usually arise in the aerial stratum of mycelium, although some extend down into the medium. The primordium is usually limited by a brown outer layer only along the upper part. One case was seen in agar culture where a brown line had formed deep in the agar below the pycnidium. Cavity formation in the pycnidia is initiated at several points, more or less in the same plane, by the appearance of slit-like openings which soon develop conidiophores all around their surface. Thereafter the cavities may become confluent to form a single cavity with an irregularly lobed or convoluted outline. The pycnidium when mature may have a diameter of 300—600 μ on both agar and clover stems.

On clover stems the primordia arise within the cortex and rupture the tissues as they increase in size (Pl. 3, fig. 1) just as they do in *Phomopsis arctii*. In *P. coneglanensis*, too, there is a constant tendency for several primordia to become confluent (Pl. 3, fig. 2) thereby resulting in uniformly large pycnidia. The periderm remains unruptured until the formation of the papillate ostiole on the mature pycnidium. Evidently this restriction by the epidermis has some effect on the nature of the pycnidium for it is evident that the fungous tissue is far more compact than when on agar and also the cavity is not so irregular in outline. There has been nothing found as yet to indicate that the slit-like cavity originates by the shearing or pulling apart of the tissues at the center as reported by Dodge (24, p. 751) for *Schizoparme straminea*. On the contrary it is more evident that the cavity arises purely by lysigenetic action along a row of cells (Pl. 2, fig. 3). Even after the main cavity has formed it is often seen (in agar cultures) that lateral extensions from this cavity arise in the same manner.

General discussion of the genus Phomopsis. The genus, perhaps due to the parasitic nature of its species and also perhaps to the production of two sorts of spores, has received rather more than its share of attention from mycologists. Many of the species have been illustrated, for example, Diedicke (20), Harter and Field (36) and Harter (34 and 35), so there seems to be good foundation for the genus, especially when one considers cases of actual connection by cultural means with the perfect stage *Diaporthe*. (See Wehmeyer 104 and 105, Harter 36, and Brefeld 11, p. 34—39). The monographic treatment too, by Diedicke (20), von Höhnel (40, Fragm. 87) and Grove (31) makes it unnecessary here to deal minutely with the genus. Instead it would be more to the point to indicate the main discrepancies in the accounts of these authors regarding the nature of the fruit body. These discrepancies have to do mostly with the definition of stroma, and will be discussed subsequently.

The presence of the two types of spores in *Phomopsis* has never been fully explained and, indeed, the diverse data on the subject, as presented by various workers, indicate the difficulty of any good explanation. Diedicke (20) considered them to be distinct types or even spores respectively of separate fungi, and reported them usually as being borne either in separate pycnidia or at least in separate portions of the same pycnidium. Later (23, p. 241) he speaks of them as merely forms and in the case of *Phomopsis arctii* (23, p. 246) where he finds both types together with all stages of intergradation he explains the difficulty by saying that the species is to be considered abnormal. This of course does not coincide with the views of Brefeld (13, p. 346). von Höhnel (40, p. 679) states that the pycnidia of Phomopsis may contain either the filiform or the fusoid spores, or if both occur in the same pycnidium there are transition forms between the two. Wehmeyer (104, p. 249)

states in the case of the pycnidial stage of *Diaporthe oncostoma* (Duby) Fuckel, that "the hamate type seems to be produced first, ... and is followed by spores of the fusoid type." This agrees with the facts presented here for *P. arctii*. On the other hand, Brefeld (11, p. 36) is of the opinion that the fusoid spores precede the filiform type and he cites a large number of examples. In agreement with this are the facts presented by Harter (35, p. 493) for the pycnidial stage of *Diaporthe phaseolorum*; although this author (l. c. p. 482) suggests that perhaps the filiform type is associated with a lack of food supply. No doubt the matter can be explained on a physiological basis but to determine which particular factor or factors are concerned can be done only by means of carefully controlled experiments with a large number of species of *Phomopsis* in culture.

So far as could be determined all the more recent writers have reported uniformly that the filiform type of spore did not germinate. Opposed to this is the ready germination of the filiform spores of *P. arctii* and it might be interesting to note that Brefeld (11, p. 37) reported the germination of the filiform type in several species.

This genus in common with many others has been grossly misrepresented with respect to the stroma. von Höhnel (40, p. 679) in speaking of the pycnidial stage of *Diaporthe* states: — "Diese Behälter der *Diaporthe*-Arten sind leicht kenntlich. Es sind Hohlräume im jungen Stroma, die vor der Entwicklung der Perithezien entstehen und keine eigene Wandung besitzen, können daher nur als Melanconieen betrachtet werden." Evidently he did not retain this idea, for in his key (50) the genus does not appear under the Melanconiales. Diedicke (20, p. 17) describes the structure as follows: "Gewiß sind sie nur Hohlräume in einer Art von Stroma, — aber dies Stroma geht, solange die *Phomopsis*-Sporen vorhanden sind, überhaupt nicht weiter, und ich habe deswegen das Ganze als sklerotiales (stromatisches) Gehäuse bezeichnet; es ist ungefähr der Begriff des pseudopyknidialen Gehäuses von Potebnia." It has been demonstrated already (p. 16) that Potebnia misinterpreted greatly the nature of the so-called pseudopycnidium. Furthermore Potebnia did not consider his pseudopycnidium to be stromatic yet Diedicke states that the "sklerotiales (stromatisches) Gehäuse" is approximately the pseudopycnidium of Potebnia.

Harter and Field (36, p. 10—11) referring to the pycnidium of *Diaporthe batatatis* state: "A stroma is not found on the stems, petioles, or leaves", but that on the roots — "the pycnidia are imbedded in a well-developed stroma." However when one examines the figures (l. c. Pl. 3, fig. 2 and 6) it is quite evident that they have mistaken locules for pycnidia. They have considered the more or less well developed layer surrounding the cavities to be pycnidial walls. It is exactly at this point that so much of the confusion has arisen regarding so-called stromatic

fruit bodies (see p. 73). This layer is not the pycnidial wall but it is merely a meristematic tissue that gives rise to the hymenial layer and is fully explained in connection with *Sphaeropsis* (p. 31) and *Cytospora* (p. 24). The real explanation of the so-called "stromatic" development of the pycnidia on fleshy roots as opposed to the "absence of stroma" on the leaves and stems lies in the fact that the morphology of the fruit body is influenced, to a certain extent, by physiological environment. In the fleshy roots there is richer food and more moisture than in the leaves or stems. These two factors are conducive to the production of not only more primordia per unit area but also to larger primordia. Many contiguous primordia will fuse to form a solid mass of tissue with a common, enveloping, brown layer. Cavities will arise at various points and if moisture conditions remain favorable they will enlarge and finally become confluent to form a single, large irregular cavity but if the substratum suddenly dries out then the development will cease, the cavities remain separate and one obtains just such a structure as presented by Harter and Field (l. c. fig. 2). This same explanation for stromatic development would apply to the results obtained by Taubenhaus (97) in his experiments with several Diplodias. Shear (86, p. 27) and Anderson (2, p. 24—25) have indicated that the size of the fruit body, i. e. stromatic development, is influenced both by the nature of the substratum and the amount of moisture.

Cytospora minuta Thüm.

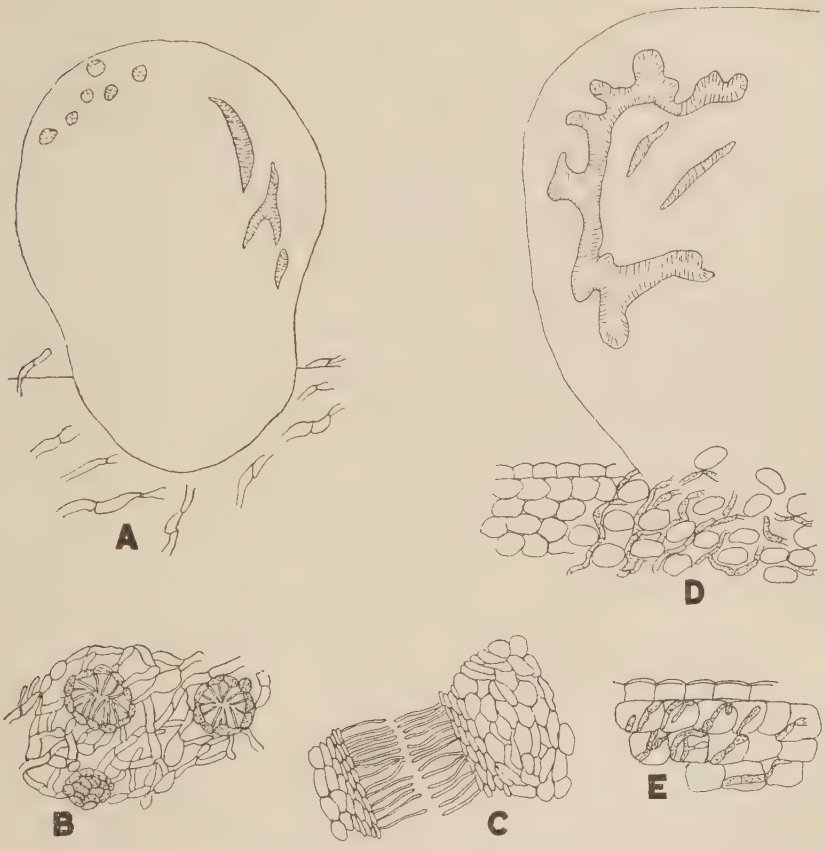
On the host. Fruit bodies scattered or evenly distributed, elevating the upper layer of the cortex and the periderm in rather large papillate mounds, remaining covered with the exception of the apex of the snuff-brown disc, through which there projects the glistening black ostiole. Vertical sections show that the fruit body (1,5—2 mm) is embedded in the cortex and consists of several separate and distinct cavities (300 μ basal diam.) connected by their necks which are confluent with the apical central ostiole (text fig. 5, A). A few pycnidia are found with only one locule (text fig. 5, C) and these have an unique ostiole, much like that described for *Cytophoma pruinosa* (p. 29). Occasionally there was found a younger structure with no cavity and consisting only of fungous tissue and intermixed cortical tissue. The ostiole and necks are embedded in a mass of browned pseudoprosenchyma tissue, while the lower portions, i. e. the more or less radially arranged cavities are embedded in a grayish-brown mass of tissue consisting of disintegrated cortical cells and fungous hyphae, the latter corresponding to the remains of the primordium. The cavities are bounded by a distinct blackened layer of elongated cells (the meristematic tissue) and are easily separable from the surrounding host tissue. The circumference of the cavity is regular, unbroken by convolutions or projections of the wall. The simple or basal-branched conidiophores arise

thickly all around the cavity and abstrict cylindrical, curved, hyaline spores, measuring, 5—6 ⩽ 1 μ. There was present an associated *Valsa*.

Cultural characters. The middle stratum is thin and transparent; the aerial is absent; the surface of the culture has a moist appearance. The pycnidia are at first immersed but later are almost entirely erumpent on both agar and clover stems. In tube cultures spore horns form in the drier parts of the medium, but under moist conditions the spores ooze out in a watery mass. The fresh horns are canary yellow, changing to a pale amber.

Paraffin sections. In the clover stems the hyphae are widespread, and are distinctly seen penetrating throughout the cortical cells (text fig. 4, D—E). On the agar, too, the hyphae tend to be sparse, not forming the usual thick middle stratum seen in cultures of other fungi. The primordium arises as a small, rather compact knot of hyphae just below the surface of the agar or clover stem at a point on some one of the ramifying hyphae. This now enlarges to form a globose structure of pseudoprosenchymatous tissue, about 300 μ diameter, or, more often when several primordia form in close proximity (Pl. 4, fig. 1), they may all fuse together to produce perhaps a still larger mass of tissue. After a time a certain stage (Pl. 4, fig. 2) is reached in which numerous giant cells appear, evidently of the same nature as reported for *Cytophoma pruinosa* (p. 29). Thereafter subsequent enlargement is accomplished by the proliferation of the outer peripheral layer of tissue (Pl. 4, fig. 3), with the exception of the basal portion embedded in the substratum. The primordia attain considerable size (500 μ diameter) before cavity formation ensues. Then at several points, usually aligned near the upper periphery (text fig. 4, A) small circular areas having a strong affinity for stain are seen; within each of these areas a minute cavity (about 10—20 μ diameter), lined with conidiophores, appears (text fig. 4, B). The tissue within which these cavities arise may be rather loosely woven as compared with the basal portion. In other words the cavities arise before the hyphae composing this tissue have proliferated sufficiently to form a compact mass and there is good reason to believe that the general dimensions of the structure increase considerably for an indefinite time, even after cavity formation. A given cavity enlarges irregularly, soon becoming confluent with similar neighboring cavities to form a continuous, more or less convoluted hymenium (text fig. 4, A). At this time the cavity is surrounded by a distinct sub-hymenial or meristematic layer of tissue (text fig. 4, C). It is this layer that preserves the meristematic function of pushing out conidiophores into the cavity and at the same time continually recedes so as to involve additional adjacent primordial tissue, thus giving rise to an ever increasing cavity. It is this sub-hymenial layer that becomes brown in the mature fruit body on the host and which is commonly misinterpreted as the pycnidial wall. This merging of the peripheral cavi-

ties sometimes results in the isolation at the center of the primordium of a portion of tissue which may also contain other cavities (text fig. 4, D) but the constant origin of new cavities and the fusion of the older ones subsequently uses up all the interior tissue of the structure leaving finally



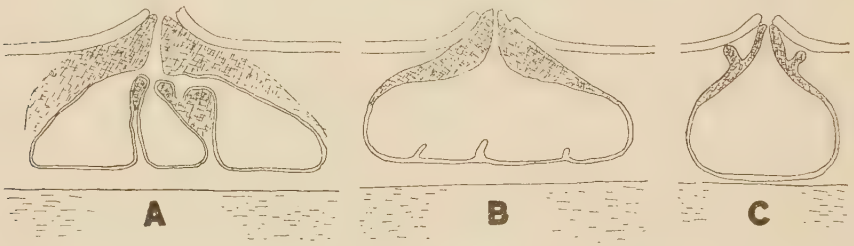
Text fig. 4. *Cytospora minuta* in culture.

A Young pycnidium on agar at time of cavity origin. Cavities at left are young, those at right are more mature. B Portion of pycnidium enlarged to show details of cavity origin. The lower body is a stage just prior to the formation of the cavity, while the upper two represent young cavities lined with spores. C Portion from *A* enlarged to show detail of more mature cavity. The small cells next to the spore layer represent the meristematic tissue. D More mature pycnidium on clover stem with cavities confluent to form a convoluted hymenium. E Detail of portion of clover stem to show intracellular hyphae. (Vide Plate 4.)

only a single large cavity with a ragged outline. A definite blackened outer layer enveloping the fruit body, as found commonly in the *Sphaeropsis* type of pycnidium, is never formed but this is readily explained when one compares the two types of primordia. In the *Sphaeropsis* primordium, for instance, when the oxidation process occurs forming the brown envelope there is little chance of air penetrating to the interior because

of the dense nature of the pseudoparenchymatous tissue and consequently only a few layers of cells on the exterior are affected. On the other hand the *Cytospora* type of primordium consists of comparatively loosely interwoven hyphae, so that the free penetration of air results in an uniform oxidation and browning throughout the tissue. In such a structure it is to be noted that the only distinct continuous layer is the meristematic tissue immediately surrounding the cavity, so when this layer becomes oxidized and brown it is quite noticeable in the mature fruit body on the host and is ordinarily, through quite incorrectly, considered to be the pycnidial wall.

Comments on exsiccati. Thümen's original description of *Cytospora minuta* states that the spores are straight and the pycnidia gregarious but an examination of Mycotheca universalis no. 890, shows that the spores are allantoid and the pycnidia separate and one-loculed. *Cytospora minuta* Thüm., in Sydow Myc. germ. no. 919, shows the same fact with the



Text fig. 5. *Cytospora minuta* on host.
A Many-loculed fruit body from large branch, with stromatic tissue above and between the locules. B Ditto, in which the locules have become confluent. C Single-loculed fruit body from twigs and smaller branches.

exception that a few pycnidia on a large twig are many-loculed. Furthermore in both of these exsiccati the pycnidia have a typical enlargement at the apex exactly like the structure described and illustrated by von Höhnel (43, p. 133) and discussed (p. 29) in this paper for *Cytophoma pruinosa*. As a matter of fact the pycnidia of *Cytophoma pruinosa* can not be dinstinguished readily from the smaller, one-loculed forms of *Cytospora minuta* by ordinary microscopic examination, but the two species do differ in cultural characters, in mode of cavity formation and in the fact that *Cytospora minuta* often has larger pycnidia with several locules. *Cytospora pulchella* Sacc., in Sydow Myc. germ. no. 89, is the same as *Cytospora minuta* Thüm. The specimens examined were on large twigs and therefore most of the pycnidia were many-loculed, although a few with one locule were found. The spores measured 4—5 $\leqslant$ 1—1,5 μ. The descriptions of *Phoma infossa* E. & E. and *Cytospora annularis* E. & E. indicate that they are also synonyms of *Cytospora minuta* Thüm. The distinguishing character of *Cytospora annularis* is the white ring around the ostiole, but in the herbarium of the University of Michigan there is a

specimen from Ann Arbor, labeled *C. minuta*, which has these distinguishing white rings. The material is overmature, indicating that the rings appear with age. There is also another local collection labeled *Phoma infossa* E. & E. that has an associated species of *Valsa* (cf. Ellis 25, p. 102). In this collection the fruit bodies are quite variable; those on the smaller twigs are one-loculed and measure 500 μ in diameter; others are larger (2 mm. diameter) with an irregular cavity (text fig. 5, B); while those on the larger twigs also measure 2 mm. diameter but have several well defined locules. It is evident that those pycnidia with a single irregular cavity formerly had several separate locules which became confluent to form a single cavity; and this conclusion is well corroborated by the presence of irregular projections, at the base of the cavity, which suggest the remains of partitions between the formerly distinct locules. In general it seems clear that those fruit bodies arising on older, larger branches are inclined to form large, many-loculed (composite) pycnidia; while those on the younger twigs are inclined to form small, one-loculed (simple) pycnidia and in this latter condition are commonly known as *Phoma infossa* E. & E. The synonymy of the species so far as investigated is to be considered as follows:

Cytospora minuta Thüm.

Phoma infossa E. & E.
Cytospora annularis E. & E.
Cytospora pulchella Sacc.

General discussion of the genus Cytospora. The difficulty is not so much in deciding what fungi belong to the genus but rather in distinguishing between species. As in *Sphaeropsis* and *Camarosporium* there are many described species differing only in the host or often in some very minute character, such as length of spore. The genus *Cytospora* is another example of misinterpretation of structures and in order to make matters clear it will be necessary first to correlate the pycnidial structure in culture with that in the tissues of the host. In the first place there is the difference in shape which needs little explanation since it is conceivable that the pycnidium arising within the cortex is restricted in its development by the surrounding host tissues, and thereby caused to take on the compressed shape as seen in text fig. 5, A—B. The primordium, as it developed in the agar, was seen to increase in size by the proliferation of projecting hyphae (Pl. 4, fig. 2—3). Now this same mode of enlargement occurs in the host; the hyphae from the periphery of the young primordium penetrate into the surrounding cortex, disrupt the tissue and gradually dissolve the cells. It is these penetrating, dissolving hyphae intermixed with the disintegrating cortex, and not the meristematic layer (cf. p. 24) which correspond to the true pycnidial wall (stroma). After cavity formation is initiated the meristematic layer extends its limits as fast as the advance hyphae dissolve away the impeding cortical tissue.

When the particular set of conditions necessary for the dissolving action of the hyphae ceases, there can be, likewise, no increase in cavity size and the development is halted. Therefore we could consider text fig. 5, A as an arrested stage of the development toward the structure in text fig. 5, B. The entire developmental story is strikingly similar to that given for the pycnidial stage of *Endothia parasitica* by Anderson (2, p. 21—23) and suggested for *Phomopsis arctii* (p. 19) in this paper. To explain the development of small, one-loculed pycnidia on the young twigs and large, many-loculed pycnidia on larger branches the writer suggests for the latter case that more primordia became fused to form the composite pycnidia and also that perhaps developmental conditions were more favorable. Anderson (l. c.) has remarked on the great effect of moisture upon stromatic development.

von Tavel (98, p. 119) in his studies with "*Cytispora platani*" Fuck. considered correctly that many-loculed pycnidia arose by the merging of several primordia at a young stage but he incorrectly (l. c. p. 118) interpreted the stratum of hyphae seen on the agar surface to be the stroma and on the host he wrongly considered the locules as the pycnidia and the tissue surrounding them to be the same as the middle stratum seen on the agar surface. This stratum is the purely vegetative mycelium formed on the agar surface and is a cultural characteristic of a great variety of fungi, even in groups outside the Fungi imperfecti. (It was not especially distinct in the cultures of *Cytospora minuta*.)

Grove (33, p. 1—2) labored under the same delusion as did von Tavel, regarding the true nature of the fruit body. He considered the locules of the fruit body to be the pycnidia. He states: "The pycnidial chambers, or chamber, of *Cytospora* always arise in a stroma (sometimes, however, nearly obsolete) .... The stroma, ... is covered by the epidermis or periderm which it usually raises convexly; sooner or later it becomes erumpent, conical or pustular, enclosing one or more chambers (pycnidia), which are often imperfectly separated and irregular or sinuous in shape (loculi), ..." This shows the absurdity of terming the same structures "pycnidia" at one time and "loculi" at another.

Diedicke (23, p. 327) considers the morphology of the stroma to be the only reliable character and therefore cites various degrees of irregularities in the cavities for determining differences between species. Judging from the mode of pycnidial development seen in *Cytospora minuta*, however, it seems possible that these various differences in the shape of the cavity, as used to distinguish between species, might be due to the physical nature of the host tissue rather than to the inherent nature of the fungus. This indicates the danger of depending solely upon exsiccati for interpretations. A particular collection gives, usually, only one stage in the development of the fruit body and furthermore there is no way of deciding from the specimen what effect the bark or cortex tissues have

had upon the nature of the cavities. It is therefore essential that the development of the fungus in culture be carefully studied before general interpretations can be made regarding any great numbers of the so-called species of this genus.

Cytophoma pruinosa (Fr.) v. H.

On the host. The pycnidia are rather thickly scattered, and are immersed in the cortex with only the ostiole erumpent through the slightly arched periderm. The pycnidium is globose, or slightly depressed, with a wall (20—40 μ thick) made up of brownish, thick-walled cells. The conidiophores line the entire surface of the simple cavity. At the top of the pycnidium there is a mound-shaped mass of buffer tissue (cf. von Höhnel 43, p. 133, fig. 31) consisting of rather loosely aggregated, elongated, or irregular-shaped, brown cells. Evidently it is this buffer tissue that effects the upheaval of the periderm. Within this buffer tissue there is found, enclosing the ostiole canal, a triangular-shaped area of tissue demarcated from the buffer tissue by a black line. It consists of smaller, more closely aggregated cells, and to all appearances arises from hyaline tissue near the cavity and grows through the buffer tissue.

Cultural characters. The middle stratum is thin, white and translucent; aerial, absent, except for whitish wefts around each pycnidium. The mycelium is very tough, making it difficult to separate out portions for transfer. There is a farinaceous odor present like that characteristic of some mushrooms. The embedded pycnidia occur abundantly in the medium and quite sparsely on the clover stems and then are much smaller. No spore horns are formed.

Paraffin sections. On stems the primordium forms well below the surface of the epidermis and then as the primordium increases in size the cortical tissue and the epidermis are pushed up in a mound-like mass and are not ruptured until the ostiole formation ensues. On agar the primordia likewise form below the surface and become semi-erumpent with maturity. The primordium is evidently symphogenous in origin because its tissue is plectenchymatous; the walls quite evidently consisting of closely interwoven hyphae. Also the young primordium, shortly after its formation consists of a tight knarl of hyphae. The cavity formation ensues at a very young stage in the development of the primordium by dissolution of the central tissues and is preceded by the appearance of a few giant cells, which are nothing more than scattered hyphae that have become swollen four to six times the normal size. As this dissolution proceeds, enlarging the diameter of the cavity, the primordium also is being enlarged by the growth and addition of outer layers of hyphae. As the cavity increases it is occupied by a gelatinous substance, — homogeneous at first but finally vacuolated. During the process of increasing in size the pycnidium is also being forced upward until finally it is more

or less erumpent. Some time during this period of growth, after the cavity has attained considerable size, there is formed a dense growth of long, slender, radially arranged, ingrowing hyphae (conidiophores) that occupy most of the space in the cavity, though usually there may be a small vacant space at the very center. Then the walls become browned, first at the top and sides and finally at the bottom, a procedure which indicates that the browning is an oxidation process. At any rate this browning is a factor in the maturing of the pycnidium for after it takes place there seems to be no increase in the dimensions of the structure and furthermore spore formation ensues.

Shortly after the browning of the wall the long, closely packed, radially arranged conidiophores break down into spores leaving a cavity filled with loose spores and a lining of short, branched conidiophores; like those ordinarily seen in mounts from the mature pycnidium on the host. It is not certain that the conidiophores do break down into spores, simultaneously along their entire length, but it does seem certain that the abstriction of spores is very rapid, occuring in a very short space of time.

Coincidently with spore formation or perhaps even before, there are signs of ostiole formation. Internal pressure first succeeds in causing a disruption and proliferation of the wall tissue at the apex of the pycnidium to form the mound-shaped buffer tissue. The ostiole development then proceeds in the way already indicated for the pycnidium on the host. This mode of ostiole formation is evidently found in other fungi, judging from the facts presented for the one-loculed pycnidia of *Cytospora minuta* (p. 23) and also from the description and illustration given by Dodge (24, p. 752, Pl. 5—6) for *Schizoparme straminea* Shear.

The chief distinction of the genus as originally described by Saccardo was the *Phoma*-like structure and the branched conidiophores. Diedicke (23, p. 193) mentions other genera, i. e. *Macrophoma* and *Pyrenochaeta*, that may also have branched conidiophores, but he considers *Dendrophoma* to be easily distinguished by its small spores, the single-chambered pycnidium and the completely browned wall. von Höhnel (43, p. 132) considered *Dendrophoma pruinosa* to be a stromatic fungus because of the development of the ostiole tissue at the top of the pycnidium and on the basis of this he established the new genus *Cytophoma*, with *Dendrophoma pruinosa* as the type. He considered it to be closely related to *Cytospora*, differing principally in the simple cavity. This is merely another application of an exaggerated distinction of stroma used by von Höhnel to establish so-called stromatic genera. This attempt to prove the presence or absence of stroma is obviously futile from the standpoint of the new conception of stroma (p. 73). The genus *Cytophoma*, however, does bear close resemblance to *Cytospora* in certain microscopic characters, such as the giant cells in the primordium, the mode of ostiole formation and the shape of the spores.

B. Phaeosporae-Phaeodidymae.

Sphaeropsis conspersa (Schw.) comb. nov.

Sphaeria conspersa Schw.
Diplodia conspersa (Schw.) Cooke
Sphaeropsis robiniae E. & B.

On the host. The fruit bodies are thickly scattered to closely gregarious, sometimes arranged in a linear manner, and then often fused together. The pycnidia remain covered by the epidermis, so that only the scarcely visible ostiole is erumpent. The pycnidial walls are 20—30 μ thick, composed of brown, large-celled parenchymatous tissue with an outer layer consisting of blackened and thickened cells, the inner tissue being brownish. When the pycnidia are mature there is formed at the top a rather broad papillate buffer tissue of thin-walled brown cells, which breaks through the epidermis, resulting in an ostiole. At the sides and bottom the wall tissues are sometimes intermixed with disintegrated cortical cells. The spores are brown, 16—22 × 8—11 μ, 1-celled, borne on conidiophores which are about the same length as the spores. Occasionally a 2-celled spore is found.

Cultural characters. The thick middle stratum is at first white, then black; aerial, scanty, woolly and grayish; submerged, ramifying, hyaline to brown. The fruit bodies are abundant and form even in the aerial stratum. The spores are brown, mostly 2-celled; a very few are 4-celled.

Paraffin sections. The primordia consist of parenchymatous tissue, and arise below the surface of the agar but later, at about the time of cavity formation, they are nearly superficial; while on clover stems they are almost entirely immersed. Cavity formation is preceded by a definite change in the staining property of a small area of tissue at the very center of the primordium. This area of tissue forms a vacuolated, gelatinous substance and soon afterwards the cells immediately surrounding the cavity take on a meristematic function and begin to divide to form a ring of small cells. It is from these cells that the conidiophores arise and push into the gelatinous substance to form the spores (cf. Pl. 5, fig. 1 of *Sphaeropsis gallae*). This meristematic layer moves toward the outer periphery involving the surrounding primordial tissue and forms spores from its inner surface as it proceeds. In the meantime the outermost layers of primordial cells, i. e. those exposed to the air, have become browned and thick-walled to form an enveloping wall. This blackening and thickening of the outer cells seems to be connected somehow with an oxidation process, for the tissues embedded in the medium or the stems do not ordinarily undergo this change. The cavity may be irregularly lobed at first but eventually all the inner tissue is used up, resulting in a simple cavity.

The buffer tissue seen on the host is evident in culture on only a few of the more mature pycnidia. The ostiole is seen to form through this buffer tissue by a dissolving action.

Remarks on the species. The original description of *Sphaeropsis robiniae* E. & B. gives the pycnidia as sparse. In the writer's collection their distribution was variable but in general rather dense, while in culture they were sparse and separate. The presence of a very few 1-septate spores on the host and their abundant production in culture relates the writer's collection to *Diplodia conspersa* (Schw.) Cooke.

Sphaeropsis hyalina (B. & C.) Sacc.

Phoma hyalina B. & C.
Macrophoma hyalina (B. & C.) Berl. & Vogl.
Sphaeropsis pennsylvanica B. & C.
Sphaeropsis phomatella Peck
Sphaeropsis biformis Peck
Sphaeropsis fertilis Peck
Diplodia infuscans E. & E.
Diplodia rhizogena E. & B.
Sphaeropsis nubilosa E. & B.

On the host. The pycnidia are scattered, immersed in the cortex, then erumpent but remaining covered by the ruptured epidermis. The ostiole is round and merely an opening in the upper part of the pycnidial wall. The latter is characteristically blackened on the outside and brown parenchymatous within. The spores are brown, 1-celled, elliptical, and measure 17—21 × 8—12 μ. A few are curved. It is possible to find some spores that are 1-septate, especially by examining material from near the ostioles of pycnidia that have discharged some of their spores. The septate spores are a shade darker than the non-septate ones, a fact that was observed by the writer in all species of *Sphaeropsis* so far examined.

Cultural characters. The middle stratum is at first thin and brown, with a greenish tinge but later thick and black; aerial, woolly and gray; submerged, colorless and ramifying. The pycnidia arise densely over the media, and mature earlier on the stems. Under certain conditions, i. e. low temperature, the pycnidia are suppressed and only hyaline chlamydospores are found. The development of the spores was not followed at room temperature but judging from the results with other species of *Sphaeropsis* in culture and the presence of 2-celled spores on the host it is safe to assume thay eventually would be 2-celled in culture.

Paraffin sections. Most of the primordia are embedded just below the surface of the agar, with a few at a lower level. The general appearance and pycnidial development is the same as for the preceding species.

Examination of exsiccati and remarks on the species. There are eight species of *Sphaeropsis* reported on *Fraxinus* in America, the descriptions differing, as a rule, only in spore measurement or color. *Sphaeropsis fertilis* Peck, in Ellis & Ev. N. Amer. Fungi no. 3548, differs in no respect from the writer's collection save in the difference of host, the former occurring on *F. viridis*. No entirely septate spores were found in this particular specimen of *S. fertilis* but many were found in which the protoplasmic contents were divided at the center; indicating a step toward actual septation. Also there have been reported on this same host and from the same locality two other fungi, *Sphaeropsis nubilosa* E. & B. and *Diplodia rhizogena* E. & B., both on exposed roots. The *S. nubilosa* differs from the others only in septation of the spores. The descriptions of the other species intergrade and overlap and obviously have to do with mere variations of the same fungus. In the writer's judgment the synonomy stands as given above.

Sphaeropsis propullans (Schw.) Peck

Sphaeria propullans Schw.
?Botryosphaeria propullans (Schw.) Cooke
Cytoplea propullans (Schw.) Starb.
Sphaeropsis celastrina Peck
Diplodia celastri Cooke
Diplodia celastrina E. & E.
Botryodiplodia celastri (Cke.) Sacc.

On the host. Most of the pycnidia are single but a few are grouped and then more or less fused. The ostiole is merely an opening in the upper part of the wall, at which point there is sometimes a proliferation of buffer tissue. A few of the spores present have a septum at the center. In some of the older pycnidia there were observed paraphysis-like hyphae projecting above the spores in the hymenial layer.

Cultural characters. The middle stratum is at first thin and white, later thick and black; the aerial is fluffy and white, changing to grayish brown; the submerged is dense, not ramifying. Pycnidia appear abundantly on the medium after seven days but only sparsely on clover stems. The pycnidia are soon filled with brown, 1-celled spores but after two weeks in culture these are exuded in a loose mass, and then are seen to be largely 1-septate. Upon germination the germ tube ruptures the brown exospore in an irregular manner.

Paraffin sections. Sectioned material indicates that the cavity and spore development is the same as described for *S. conspersa*. In like manner the pycnidia are about half-immersed in the medium and on the clover stems they are entirely immersed in the cortex but push up the epidermis just as they do on the natural host; and also there is evidence of the proliferation of buffer tissue just before ostiole formation.

Discussion of Sphaeropsis propullans. The fungus in Ellis & Ev. N. Amer. Fungi no. 3362, issued as *Sphaeropsis celastrina* Pk. is nothing more than an immature *Diplodia celastrina* E. & E. Nearly all the spores of this specimen show faint traces of a cross-wall, i. e. it is just in the process of formation. Some of the pycnidia are aggregated and more or less fused as in the writer's own collection. A specimen originally described as *Diplodia celastri* Cooke was later changed to *Botryodiplodia* by Saccardo because of the more or less fused pycnidia. In some of the older pycnidia of the writer's collection there were found elongated hyphae extending above the spores in the hymenial layer. The same thing, described and illustrated by Starbäck (91, p. 81, fig. 59c), led to the description of the fungus as *Cytoplea propullans* (Schw.) Starb. These pseudoparaphyses are most probably nothing more than elongated sterile conidiophores. Although Sollmann (90, p. 191) describes them in *Sphaeropsis visci* as elongated conidiophores which have lost their spores. The latter explanation is unlikely in the present case for under those circumstances one should occasionally find a few spores still attached and the scar at the top of the conidiophore would be visible. Instead one finds that these structures are quite slender, about half the width of the normal conidiophores and that the apex instead of being flattened is somewhat swollen, giving the impression of abortive spores; this indeed is the interpretation given by Bauke (6) for his *Diplodia* on *Cornus*. von Höhnel (47, p. 142) says that these structures are frequently reported in various species of *Sphaeropsis* but since their presence is quite inconstant, they have no diagnostic value.

Sphaeropsis glandulosa Cooke

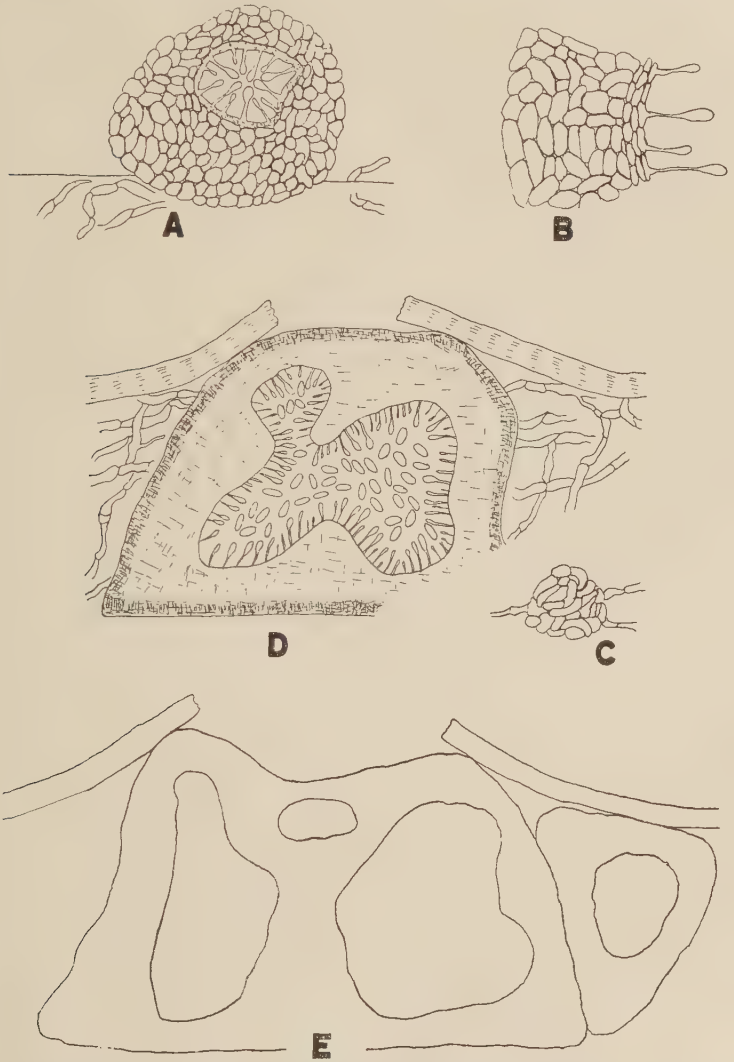
Diplodia ailanthi Cooke
Botryodiplodia ailanthi (Cke.) Sacc.
Dothiorella glandulosa (Cke.) Sacc.
Sphaeropsis ailanthi E. & B.

On the host. The material is rather young so that the cavity in some of the pycnidia is small and irregular in outline (text fig. 6, D). At the top there develops a rather broad buffer tissue, through which the ostiole forms. It is rather common to find 2-celled spores, especially outside the ostiole of the older pycnidia. The pycnidia tend to aggregate in groups of three to six (text fig. 6, E).

Cultural characters. The middle stratum is at first thin and white, later thick and black; the aerial is dense, short fluffy, dark smoky-gray, changing to thick woolly, brownish-black; the submerged forms thin ramifying strands. The pycnidia are abundant on the surface of the medium and even on the submerged strands, but on clover stems they are scanty. The spores are brown and 1-septate.

Paraffin sections. The development of pycnidia and spores is the same as described for the orther species of *Sphaeropsis*. The primordia

are quite abundant and sometimes are seen to lie rather thickly side by side (Pl. 5, fig. 2—3). On agar they sometimes develop independently to form simple pycnidia (text fig. 6, A + C) but on both agar and clover stems there is evidence that several may become confluent to form a composite pycnidium (Pl. 5, fig. 2—4). In the pycnidium given in text fig. 6, B the meristematic layer surrounding the cavity is well represented.



Text fig. 6. *Sphaeropsis glandulosa.*

A Pycnidium from agar with young cavity surrounded by meristematic layer. B Detailed portion from A to show nature of meristematic layer. C Young primordium from agar. D Nearly mature, simple pycnidium from host. E Three pycnidia in a row, from host. Two are fused. (Vide Plate 5, fig. 2—4.)

Remarks on the exsiccati. The material of Ellis & Ev. N. Amer. Fungi no. 3451, *Sphaeropsis ailanthi* E. & B., has rather small, separate pycnidia, and the spores are obscurely septate, i. e. the cross wall is just in the process of formation. The description of *Dothiorella glandulosa* (Cke.) Sacc. is evidently based on a young specimen, still with hyaline spores. Cooke originally called it a *Sphaeropsis*, and most likely the lobed appearance of the young cavity lead Saccardo to place it in the genus *Dothiorella*. Only one name, *S. glandulosa* Cooke, should be recognized.

Sphaeropsis sumachi (Schw.) Cke. & Ell.

Sphaeria sumachi Schw.
Sphaeria subsolitaria Schw.
Sphaeria rhoina Schw.
Sphaeropsis rhoina (Schw.) Starb.
Sphaeropsis fibreseda C. & E.
Diplodia subsolitaria (Schw.) Curr.
Diplodia rhois Sacc.
Diplodia rhoina C. & H.
Diplodia compressa Cooke
Botryodiplodia compressa (Cke.) Sacc.
Haplosporella burnhami Dearn.

On the host. The collection from which the culture was made is on a large dead branch, with weathered and disintegrated bark. The pycnidia are slightly erumpent, thickly grouped and mostly separate, although many are confluent in groups of two to six. They measure on the average 250 μ diam., with thick, blackened outer layers of cells and are borne in the cortex just below the periderm, some with a distinct papillate ostiole, others with merely a pore-like opening. The cortex is blackened just below the periderm. The spores are elliptical, brown, 1-celled, 16—24 ⩽ 8—12 μ. A few are dark brown and 1-septate.

Cultural Characters. The middle stratum is at first greenish-gray, changing to black; the aerial is thick, woolly white, later grayish; the submerged forms long irregular strands. Pycnidia form thickly on both agar and clover stems after six days. In cultures kept in a cold room (2° C.) for six months, spores were found, ranging from hyaline and brown, 1-celled, to dark brown and 2-celled; many were nearly globose, measuring 18—24 ⩽ 15—21 μ.

The examination of the paraffin sections showed that this fungus resembles the other species already described.

Examination of exsiccati and remarks on Sphaeropsis sumachi. In the older pycnidia of *Diplodia rhois* Sacc., Sydow Myc. germ. no. 1365, the spores have oozed out and stained the bark surrounding the ostiole, and are dark brown with one septum. In younger pycnidia which have not discharged their contents the spores are brown and 1-celled. The

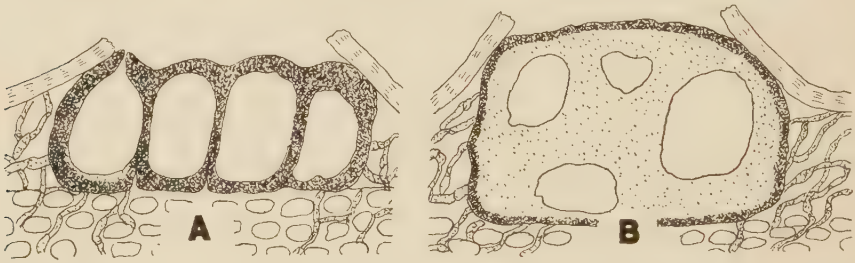
specimens of *Sphaeropsis sumachi* (Schw.) C. & E. in Ellis N. Amer. Fungi no. 29, have a few large, strongly erumpent pycnidia but most of them are small and covered by the periderm. The spores in the young fruit body are 1-celled but evidently in the older fruit body they are in process of laying down a cross wall because the spore contents are apparently divided at the center by a large vacuole. Many of the pycnidia are papillate and the cortex is blackened. Two local collections on decorticated branches, and in this respect corresponding to *Sphaeropsis fibreseda* C. & E., showed that those pycnidia with discharged contents invariably yield septate spores. Also in one of the collections there are several sticks with adhering portions of the original bark, on which there are found typical pycnidia of *S. sumachi*, with 1-celled spores. Another local collection labeled *Botryodiplodia compressa* Cke., fide Ellis, Mar. 24, 1893, has many aggregated, fused and strongly erumpent pycnidia, with narrowly elliptical, light brown, 1-celled spores, although a few are septate. On some of the smaller branches in this collection the pycnidia are less aggregated and differ in no manner from *Diplodia rhoina* C. & H., Ellis N. Amer. Fungi no. 739. The description and figures given by Currey (17, p. 284, fig. 198) indicate that *Sphaeria subsolitaria* Schw. was placed in the genus *Diplodia* on the basis of the incompletely septate spores which were of the same nature as those described above for *Sphaeropsis sumachi*, Ellis N. Amer. Fungi no. 29. The excellent description and figures given by Starbäck (91, p. 72, fig. 51 a—c) show that the Schweintz specimen of *Sphaeria rhoina* was merely a variation of *Sphaeria sumachi*. Starbäck (l. c.) points out that *S. sumachi* may have densely gregarious pycnidia, resembling *Haplosporella*, and it is quite evident that such a specimen is the basis of the *Haplosporella burnhami* named by Dearness (19, p. 354). On the basis of these studies the synonomy given on p. 36 is suggested.

Sphaeropsis gallae (Schw.) comb. nov.

Sphaeria gallae Schw.
Dothiorella gallae (Schw.) Starb.
Sphaeria glandicola Schw.
Dothiorella glandicola (Schw.) Starb.
Sphaeropsis gallae B. & C.
Sphaeropsis gallarum B. & C.
Diplodia gallae Auctt.
Dothiorella gallae E. & E.
Dothiorella quercina (C. & E.) Sacc.
Sphaeropsis quercina C. & E.
Diplodia longispora C. & E.
Botryodiplodia ostiolata E. & E.
Fusicoccum ellisii Petr. & Died.
Botryosphaerostroma quercina Petr.

The fungus on old galls as Dothiorella gallae (Schw.) Starb. This species, well described and illustrated by Starbäck (91, p. 65, fig. 44 a—c), is found quite frequently on old fallen galls of *Quercus*. Sectioned material compared with *Dothiorella quercina* and *Dothiorella glandicola* shows clearly that there is no striking difference in pycnidial structure. The spores are hyaline, 1-celled, with granular contents and thick walls but in a few of the partially disintegrated pycnidia there are found a few spores which are brown and even some that are 1-septate.

On acorns as Dothiorella glandicola (Schw.) Starb. The author's specimens agree in all respects with the original description given by Starbäck (91, p. 64, fig. 43). The pycnidia may be separate, or aggregated and then are quite often confluent like the structure in text fig. 7, A. The pycnidia are borne under the thin epidermis with the base strongly flattened against the hard outer layer of the acorn. The tissue of the pycnidium is characteristically brown parenchymatous and the ostiole is



Text fig. 7. *Sphaeropsis gallae* from host.
A Composite fruit body with locules in a row. B Composite fruit body with locules irregularly placed.

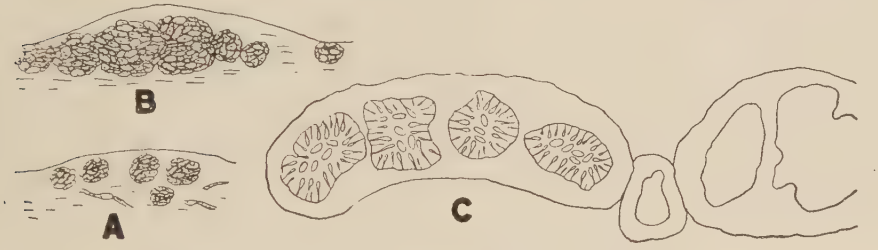
short papillate. Most of the pycnidia contain hyaline non-septate spores, with thick walls, measuring 18—21 ⩻ 14—15 μ, but a few, more mature ones, contain brown, 1-septate spores. The conidiophores average 10 ⩻ 3 μ.

On twigs as Dothiorella quercina. The local collection agrees with the specimen in Ellis & Ev. N. Amer. Fungi no. 3264. The fruit bodies are large, about 1 mm diam., black, scattered, verrucose-pulvinate, and rupture the periderm in a stellate manner. In vertical section it is seen that the fruit body consists of fused pycnidia so as to appear as locules (text fig. 7, B). The tissue is brown and parenchymatous, with the outer layer composed of blackened, enlarged cells, and the inner tissue with brown and regular cells. The spores are hyaline, thick-walled, 18—22 ⩻ 12—14 μ, borne on conidiophores of about the same length. The appearance is exactly like that given for *Botryodiplodia ostiolata*, excepting the hyaline spores.

On twigs as Botryodiplodia ostiolata. The fruit bodies are strongly erumpent, scattered, black, verrucose-pulvinate, large, averaging 1 mm diameter, and rupture the periderm in a stellate manner. In sec-

tioned material it is seen that several pycnidia have become closely confluent to form a single large fruit body, so that they have the appearance of a many-loculed fruit body (text fig. 7, A), though quite often there are smaller fruit bodies present with a single and simple cavity. There may be an ostiole for each "locule". The outer layer of tissue is blackened, while the inner portion is composed of brownish parenchyma. The spores are elliptical to broad-elliptical, brown, 1-septate, and not constricted, measuring 18—22 ⩽ 14—16 μ. Younger stages are also found in which the spores are 1-celled, hyaline, or have a slight tinge of brown, and are 1-celled, measuring slightly smaller than the septate spores.

Cultural characters. A separate culture was obtained from each of the four collections just described. No one culture differed essentially in character from the other three and for this reason all four collections are considered to be one species. In all four cultures the middle stratum is thick and brown; the aerial is grayish-fluffy; the submerged hyphae



Text fig. 8. *Sphaeropsis gallae* in culture.
A Five young primordia in agar. B Older stage in which the primordia are fusing. C Still older stage. Nearly mature, composite fruit body, with cavities arising at various points. (Vide Plate 5, fig. 1.)

form long slender strands. The pycnidia arise abundantly either on the surface of the media, or on aerial wefts and submerged hyphae, and in the last case are uniformly smaller. In cultures with layered clover stems, the pycnidia form more abundantly and mature more quickly. In young cultures the mycelium has a greenish tinge and this has been observed in all the cultures of *Sphaeropsis* species. The isolations of the three *Dothiorella* species were obtained by the ready germination of the hyaline spores but in mature cultures the three species all agree with *Botryodiplodia ostiolata* in that the spores are at first hyaline and 1-celled, while later they are brown and 1-septate. Quite often the entirely submerged pycnidia contain only hyaline, or brownish-tinged, 1-celled spores; even in 9 month old cultures.

Paraffin sections. In sectioned material it was quite impossible to distinguish between any two of the four isolations mentioned above. An examination of younger stages shows that the large primordia are formed as the result of the confluence of several smaller primordia at an early stage (text fig. 8, A—B). As they enlarge in size they form a large, more or less irregular, composite body (text fig. 8, C) with a brown enveloping

layer and characteristic parenchymatous tissue. Cavity formation then arises at several widely separated points so that a many-loculed fruit body is formed. Each locule develops a rim of meristematic tissue (Pl. 5, fig. 1), the function of which has been described on p. 31. Each locule may develop independently and produce an individual ostiole, or quite often several locules may become confluent forming an irregularly lobed cavity with one or more ostioles. In the younger cavities there is to be seen a vacuolated, gelatinous substance (Pl. 5, fig. 1) like that described for *Septoria* (p. 15). The ostiole develops after the spore formation is nearly complete and there seems to be a proliferation of the apical cells to form a papillate buffer tissue. The opening through this is formed by a dissolving action similar to that concerned in the formation of the cavity. Cavity formation is exactly like that already discussed under *Sphaeropsis conspersa* with the difference, of course, that it originates at several points.

Remarks on Sphaeropsis gallae. On the basis of the data presented above for the four "species" it is evident that they are to be considered as a single species under the suggested recombination (p. 37). Also the description of *Diplodia longispora* C. & E. as given in Saccardo's Sylloge indicates its relation to the forms presented herein. The fungus carefully described by Petrak (69, p. 301—303) as *Botryosphaerostroma quercina* Petr. is quite obviously the same as *Sphaeropsis gallae*. Assuredly there are other species, especially from Europe, which rightfully should be considered as synonyms here but one can not judge accurately from the incomplete descriptions. The fungus studied in culture by Ingram (51) is also a form of *Sphaeropsis gallae*.

Sphaeropsis visci (West.) comb. nov.

Macrospodia visci West.
Sphaeria atrovirens Chev.
Sphaeria atrovirens var. *visci* Alb. & Schw.
Sphaeria visci D. C.
Diplodia visci (D. C.) Fr.
Sphaeropsis atrovirens Lév.
Diplodia visci Kickx.
Ceuthospora visci Sollm.
Sphaeropsis visci (Sollm.) Sacc.
Diplodia phoradendri Cke.
Diplodia viscicola P. Henn.
Macrophoma visci Aderh.
Macrophoma phoradendri Wolf.
Botryodiplodia phoradendri (Cke.) Petr.
Botryosphaerostroma visci (Sollm.) Petr.

On the host. The writer's collection with its hyaline spores fits the description given by Wolf (108) for *Macrophoma phoradendri*.

Cultural characters. The fungus thrives on media, the mycelium soon becoming brown, forming a thick, brown middle stratum. The aerial stratum is at first greenish-brown, changing to brownish-gray; the submerged stratum forms long strands of hyphae. The fruit bodies are surrounded by a greenish whorl of hyphae. In the younger fruit bodies the spores are hyaline, 1-celled, with a thick exospore but when mature they are brown, 1-septate, and variable in size, measuring 25—50 × 15—30 μ.

Paraffin sections. The development and general appearance of the fruit bodies in culture are essentially like that described for *Sphaeropsis gallae* (p. 39), especially with respect to the formation of composite pycnidia.

Examination of exsiccati and remarks on Sphaeropsis visci. The production of brown, 1-septate spores in culture indicated that there might be a *Diplodia* described for this host. An examination of *Diplodia phoradendri* Cooke, in Ellis N. Amer. Fungi no. 524, collected in South Carolina on stems of *Phoradendron flavescens* is evidently the mature condition of the fungus collected by Wolf (108) on the leaves, in Texas. The pycnidium is composed of brown parenchymatous tissue and corresponds in every detail with the excellent illustration given by Wolf (l. c.). Cooke (cf. Saccardo's Sylloge) reports the spores constricted at the septum but the Ellis specimen examined did not agree with this statement. Recently there has been described by Sydow and Petrak (96, p, 208), a *Botryodiplodia phoradendri* (Cooke) Petr. on the basis of specimens communicated to them by Weir, some from South Carolina, the type locality of *D. phoradendri* Cooke, and some from Texas, the type locality of *Macrophoma phoradendri* Wolf. We have seen in the cultures of the writer's collection that the hyaline-spored form is an immature state of the *Diplodia* form and furthermore that the aggregated condition of the pycnidia is not a constant character. Therefore *Macrophoma phoradendri*, *Botryodiplodia phoradendri* and *Diplodia phoradendri* are merely forms of a single fungus.

When Wolf (108) described his fungus he made comparisons with a *Macrophoma visci* Aderh. which occurs in Europe. The description of this fungus indicates that it is nothing more than an immature *Sphaeropsis visci* (Sollm.) Sacc., which in turn is an immature *Diplodia visci* (D. C.) Fr. An examination of *Sphaeropsis visci* (Sollm.) Sacc., in Sydow Myc. germ. no. 1705, shows that the spores are of a medium brown color and that the contents of the spores consist of irregular granules with large vacuoles at the center (a sign of immaturity?); furthermore a careful search reveals a number of spores in which a cross wall has actually formed, while many others show various stages of septum formation. In addition an examination of a specimen of *Sphaeria atrovirens* var. *visci* Alb. et Schw., in Schmidt et Kunze exs. no. 76 (the same issue examined by Sollmann

90, p. 188) shows some pycnidia with the spores all septate and others in which the spores are not septate, the latter being the *Sphaeropsis* form. Sollmann (l. c., p. 191) in his detailed description of the development of the spores in *Ceuthospora visci*, states that the thick outer wall (exospore) is at first hyaline but later becomes brown and that the septum is not formed until after the spore falls from the conidiophore. Petrak (73, p. 120) refers to this same article by Sollmann when he establishes the new species *Botryosphaerostroma visci* (Sollm.) Petr., but he evidently ignores the mention of septate spores by Sollmann because he states that "Die großen Konidien .... bleiben aber dauernd einzellig". Quite obviously this conclusion of Petrak is unfounded and likewise his species name untenable. The recombination and synonomy appear on p. 40.

Discussion of the genus Botryodiplodia. Saccardo (80) established the genus *Botryodiplodia* and considered it to differ from *Diplodia* in that the pycnidia were botryose-congested on a basal stroma. Diedicke (23, p. 645) characterizes the genus as "Fruchtgehäuse traubenförmig gehäuft" but remarks that he considers the genus to be merely a growth form of *Diplodia*. Taubenhaus (97) as a result of cultural experiments with several fungi decided that certain genera were founded on inconstant characters and so emended the genus *Diplodia* to include *Chaetodiplodia*, *Lasiodiplodia*, *Botryodiplodia* and *Diplodiella*. von Höhnel (46, p. 267) describes *Botryodiplodia faginea* as: "Pykniden in kleinen Gruppen in einem lockeren oder dichteren Hyphenfilz...." and notes that the fungus can be found in the literature as *Macrophoma*, *Sphaeropsis*, *Diplodina* and *Diplodia*. Petrak (74, p. 333) states: "Das einzige, aber sichere Unterscheidungsmerkmal zwischen diesen beiden Gattungen besteht darin, daß sich die Konidien bei *Diplodia* schon sehr frühzeitig in den Gehäusen dunkel färben, während sie bei *Botryodiplodia* sehr lange 1-zellig sind, hyalin bleiben, sich meist erst nach ihrem Austritt aus den Gehäusen dunkel färben und eine Querwand erhalten." This assumption is not corroborated by the facts presented in this paper. It has already been shown that *Botryodiplodia phoradendri* (Cke.) Petr. (p. 41), *B. celastri* (Cke.) Sacc. (p. 34) and *B. ailanthi* (Cke.) Sacc. (p. 34) differ in no way from the corresponding "*Diplodia*" forms. In addition an examination of the specimen of Ellis & Ev. *Botryodiplodia gossypii* E. & B., in Fungi Columb. no. 1510, reveals nothing more than a matured *Dothiorella major* E. & E. or a form of *Diplodia gossypina* Cooke. We have seen that this distinguishing character (variously known as aggregated, fused or "traubenförmig gehäuft" pycnidia, or many-loculed fruit body) of *Botryodiplodia* is due to the confluence of contingent primordia and also it has been shown to be quite inconstant, i. e., in *Sphaeropsis propullans*, *S. sumachi*, and *S. glandulosa* the fused condition was occasionally found on some parts of the host but not in culture. *Sphaeropsis visci*, on the other hand, did form composite fruit bodies in culture, agreeing in this respect with *S. gallae*. (See also

Stevens, 93, p. 586—587.) It is seen then that *Botryodiplodia* is only a form of *Diplodia*.

Discussion of the genus Dothiorella. The genus *Dothiorella* established by Saccardo (80), was based on the same type of fruit body as that in the genus *Botryodiplodia*. i. e., aggregated-botryose on a basal stroma or else with locules sunken in a stroma. von Höhnel (47, p. 173) emended the genus to include only such forms characterized as "dothideoid gebaute, deutlich dünnwandig-offenzellige, polsterförmige Stromata mit ganz eingesenkten Lokuli". He makes no remark concerning the thickness of the spore wall but (l. c. p. 174) he gives *Dothiorella quercina* as a typical representative of the genus. Petrak (71, p. 138) in discussing *Dothiorella aesculi* says that there can be variation between the type of fruit body where the pycnidia are heaped on a basal stroma and the other extreme where there are locules entirely sunken in a stroma. *Dothiorella* differs chiefly from *Botryodiplodia* in its hyaline spores but we have seen that in *Dothiorella gallae*, *D. glandulosa* and *D. quercina*, that the hyaline, thick-walled spores germinated and produced in culture the typical brown, 2-celled spores of "*Diplodia*". It is evident that the significance of these thick walls of the hyaline spores has not been duly appreciated, for there appear throughout the literature many descriptions of species of *Dothiorella* and of *Macrophoma* with thick-walled spores. When such a species is encountered a corresponding species name is to be sought under *Sphaeropsis*, *Diplodia*, *Haplosporella* (cf. p. 45), or *Botryodiplodia*. The thick, hyaline wall, here understood as a criterion of immaturity, will eliminate many species of the genera *Macrophoma* and *Dothiorella*, leaving only those forms with hyaline, thin-walled spores. In this sense the species of *Dothiorella* mentioned by Shear, Stevens and Wilcox (87 and 88) is evidently a true representative of the genus (1).

Discussion of the genus Macrophoma. The genus was established by Berlese and Voglino, according to Saccardo's Sylloge, by the simple expedient of separating out all species from *Phoma*, *Phyllosticta*, *Sphaeropsis* and *Sphaeronema* having spores over 15 μ in length. The purely artificial nature of the genus has been mentioned by several investigators and has been proven so by others who have cultured various species. Allescher (1) speaks of the genus as "nicht sehr umfangreiche" while Diedicke (23, p. 186) concludes that the separation of the genus is entirely arbitrary and also that many of the species have thick-walled spores, but he attaches no significance to this last fact. Emerson (26) by means of culture proved the relation of a "*Macrophoma*" to a "*Diplodia*" on *Cocos nucifera*, thereby establishing the fact that *Sphaeropsis palmarum* Cooke is only an immature *Diplodia epicocos* Cooke. Evans (27, p. 10) found in *Diplodia*

(1) The writer has studied cultures and specimens generously loaned by Dr. C. L. Shear.

natalensis that the spores could be emitted in a hyaline and 1-celled condition but that under certain conditions they later become dark brown and 1-septate. Hesler (37, p. 74), in his studies on *Sphaeropsis malorum*, found in an early stage of development the *Macrophoma* type of spore, one-celled and hyaline; later the *Eu-Sphaeropsis* type, one-celled and brown; and finally the *Diplodia* form. Petrak (74, p. 314) states that the genus *Macrophoma* "gehört zu den ärgsten Mischgattungen" and that "ohne auf den Bau des Gehäuses, der Sporen und auf die Art der Konidienbildung die geringste Rücksicht zu nehmen, wurden von den Autoren alle mehr oder weniger stromalosen Formen mit größeren Konidien als *Macrophoma* beschrieben. Dazu kommt noch, daß *Macrophoma* auch als Ablagerungsstätte für viele zweifelhafte Formen dienen mußte und viele jüngere, noch hyalinsporige Entwicklungsstadien von *Botryodiplodia* und *Traversoa* enthält." Later (75, p. 108) he reports that many species of the genus are ". . . . dothideoid gebaut und unreife oder notreife Entwicklungszustände von *Botryodiplodia*-Arten."

An examination of *Macrophoma celtidis* E. & E., in Ellis & Ev. N. Amer. Fungi no. 3357, reveals an immature fruit body, with several small locules, containing hyaline thick-walled spores. This is certainly nothing more than an immature *Haplosporella celtidis* E. & E. = *Sphaeropsis celtidis* E. & E. *Macrophoma taxi* (Berk.) Berl. & Vogl., in Briosi et Cav. no. 192, shows thick-walled spores mostly with a suggestion of a brownish tinge but a good number are brown, 1-septate and constricted. Under the original description of *Sphaeropsis taxi*, Berkeley states that the species is probably an immature stage of *Diplodia taxi* De Not.; a statement that is doubtlessly correct. In the writer's opinion all species of *Macrophoma* with thick-walled, hyaline spores are to be considered as immature stages of *Sphaeropsis* species (cf. p. 43).

General discussion of the genus Sphaeropsis. Léveillé (60) states that he originally based his genus *Sphaeropsis* on a specimen which he later discovered to be a *Diplodia*. He says further: "Ces deux genres ont la plus grande ressemblance, puisqu'ils ne diffèrent, en effet, que par la présence ou l'absence d'une cloison dans le spores. Quoique ce caractère soit très léger en apparence, il est cependant dans les Clinosporés d'une grande importance; car il permet de séparer en deux groupes, au premier examen microscopique, un nombre considérable de petites espèces, qui'il serait impossible de distinguer". von Höhnel (44, p. 85) states that "Die *Diplodia*-Arten können in dem Zustande von *Phoma (Macrophoma)* oder *Sphaeropsis* verbleiben." Shear (82) found that the imperfect stage of *Botryosphaeria fuliginosa* (M. & N.) E. & E. agreed morphologically with *Sphaeropsis malorum* Peck and *Diplodia pseudodiplodia* Fuckel. Hesler (37, p. 73, 98, 99) found that all the various forms of *Sphaeropsis*, which he isolated from forty different hosts, would produce 2-celled spores. The writer finds that in culture the septation occurs mostly after the spores

have been exuded from the pycnidium and this seems to be true also in nature. Furthermore, the examination of material from various exsiccati reveals that species of *Sphaeropsis* in general have spores with a large vacuole at the center and repeated observations indicate that this vacuole is directly concerned with the septum formation; much after the fashion described by Sollmann (90, p. 190—191). Hesler (l. c. p. 100) states further: "but both genera *(Diplodia* and *Sphaeropsis)* fail in their chief distinctions, so that mycologists have been misled on this point." Diedicke (23, p. 579) says of the genus *Sphaeropsis:* "Viele Arten sind sicher nur Entwicklungsstadien von *Diplodia* oder weiter ausgebildete Stadien von *Macrophoma* . . . . Im Bau der Gehäuse stimmen die drei Gattungen vollständig überein, und es fragt sich nur, wie weit die Entwicklung der Sporen fortgeschritten (oder bekannt!) ist. Daß nach und nach diese Lücken in unserer Kenntnis durch fortgesetzte Beobachtungen in der Natur oder durch Kultur der Pilze ausgefüllt werden müssen . . . ."

Obviously the fungi described as species of *Sphaeropsis* are nothing more than immature stages of *Diplodia.* A glance through the literature of described species will show that for practically every *Sphaeropsis* there is a corresponding *Diplodia* on the same host. It is true, of course, that the spores of many species can remain brown and 1-celled under certain conditions. A series of physiological experiments should be made to determine the factors concerned in browning and septation. At any rate a *Sphaeropsis* spore should be considered as a potential *Diplodia* spore, and if we are to attain the ideal condition of having a single name for a single fungus then it is advisable either to abolish the genus *Sphaeropsis* in favor of *Diplodia,* or else to emend it to include *Diplodia.* The latter procedure is more consistent with the rules of nomenclature and the writer has followed this plan in the species concerned.

It is clear that there are concerned in the life cycle of many species of *Sphaeropsis* also certain forms which have been described under the genera *Macrophoma, Dothiorella, Haplosporella* and *Botryodiplodia.* Sometimes these are referred to as "form genera" but in the writer's opinion this is a poor usage of the term. Since they are obviously mere developmental stages of the same fungus a more correct term would be "growth forms".

Camarosporium robiniae (West.) Sacc.

On the host. In the writer's specimen some of the pycnidia were growing in and on old disintegrated fruit bodies (presumably pycnidia) of some other fungus. From general appearance the situation seems to imply the formation of a second crop of pycnidia within the older ones. The small pycnidia measure 200—300 μ but otherwise they correspond exactly with the description given by Diedicke (23) and others for *C. robiniae.* (von Höhnel, 47, p. 143, considers the three species of *Camarosporium* described on *Robinia* to be the same fungus.) Usually the

new pycnidia are surrounded by a loose weft of dark brown hyphae which spread through the spaces of the old pycnidia but in other respects the general appearance and structure of the pycnidium was the same as that of *Sphaeropsis conspersa.*

Cultural characters. The middle stratum is black; the aerial, grayish with a greenish cast, covering the pycnidia. The pycnidia mature after four weeks on both media and stems.

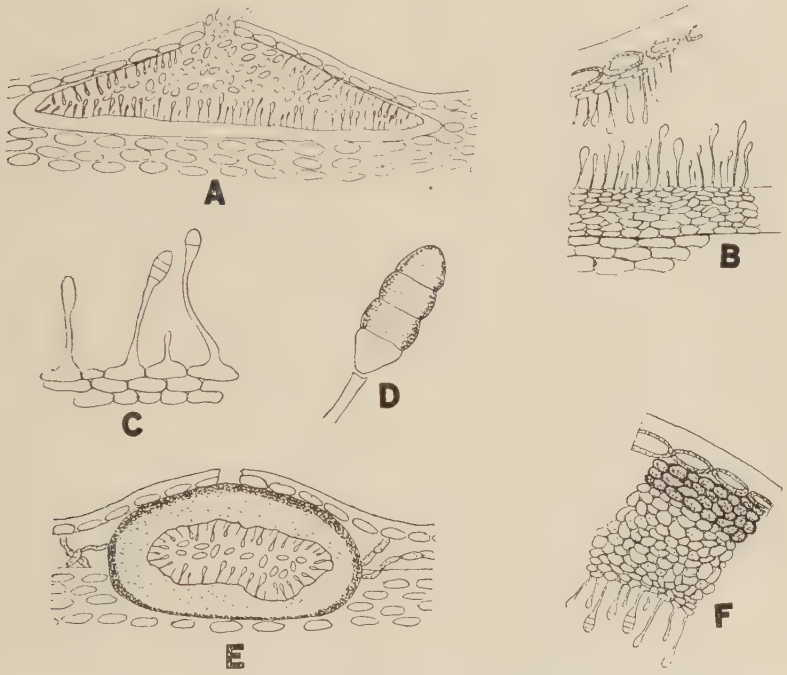
Paraffin sections. The formation of the primordium and of the cavity is essentially the same as that described for the species of *Sphaeropsis* except that the cavity is never lobed. The spores arise directly from the primordial cells, i. e. without forming a conidiophore and judging from the descriptions this seems to be characteristic for most of the species of the genus. Prior to ostiole formation there is apical growth of the pycnidium to form a papillate structure, consisting of cells much smaller than those of the pycnidium proper. Later the ostiole canal is formed through this papillate structure by dissolution of the cells.

Practically the only difference between *Sphaeropsis* and *Camarosporium* is the presence of muriform spores in the latter. Most of the species of *Camarosporium* are practically indistinguishable from one another except for the difference in the host, and it would not be at all surprising should future cross inoculations prove that many of the present species are nothing more than the same fungus growing on different plants.

Hendersonia rubi (West.) Sacc.

On the host. The fruit bodies occur sparsely scattered or grouped and are rather small (100—350 μ diam.). As they reach maturity the overlying epidermis is strongly arched and finally ruptured in a stellate or irregular manner, the ruptured fragments remaining in place to cover the fruit body at the sides; the spores then ooze out in a black mass to stain the surface of the bordering cuticle. The fruiting structure is borne in the outermost layer of the cortex, just below the epidermis, and in vertical section appears to be nearly lens-shaped (text fig. 9, A). In young stages the entire cavity is lined with fungous tissue and conidiophores, there being less tissue above than below but nearer the time of maturity there is found only a basal palisade-like layer of conidiophores arising from a rather thin layer of hyaline pseudoparenchyma, much like the structure represented in text figure 9, A. In this condition the structure is recognized as a *Coryneum.* Quite frequently, even on the same cane, another type of fruit body is found (text fig. 9, E), which seemingly occurs where the cuticle or epidermis has become loosened and where there is no tension to be overcome by the hyphae which constitute the developing primordium. This structure, readily recognized as a pycnidium, tends to be globose, with definite pseudoparenchymatous tissue, blackened without and hyaline within. The spores are borne exactly alike in both types of

fruit bodies, the conidiophores arising from a peripheral cell and enlarging at the free end to form a spore (text fig. 9, C). The upper three cells of the spore are brownish while the basal cell is usually hyaline like the conidiophore and apparently is merely a continuation of it (text fig. 9, C—D). Although there is no visible cross wall in this lower cell yet a very delicate or obscure septum must exist since the spores separate so uniformly from the conidiophores.



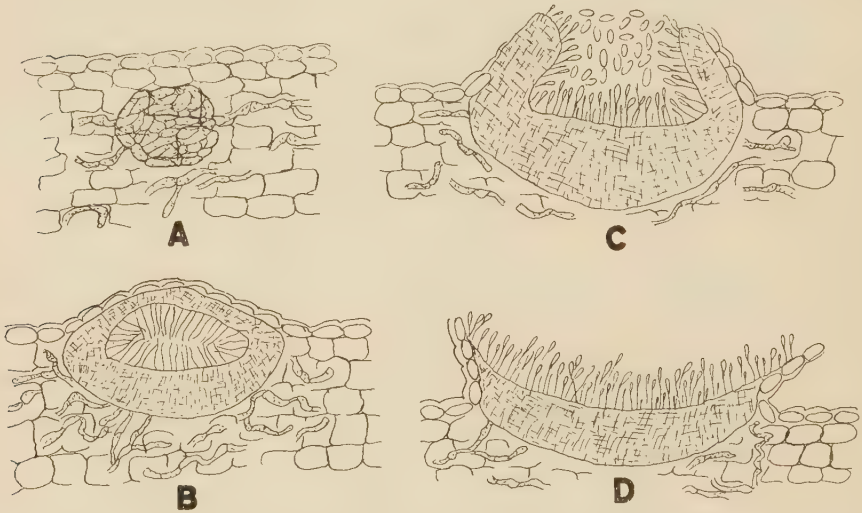
Text fig. 9. *Hendersonia rubi* on host.

A Acervulus-like fruit body. B Detailed portion from A to show thick layer of tissue below and thin layer above. C Portion of hymenial layer in B to show mode of spore origin. D Mature spore and portion of conidiophore. E Mature pycnidium with well developed wall. F Portion from E to indicate nature of the dark outer layer.

Cultural characters. The middle stratum is white, changing to light brown at the center and shading to white at the margins; the aerial is absent at first but later appears as a fluffy, dingy-white mat; the submerged produces hyphae which ramify throughout the media, forming abortive pycnidia. Mature pycnidia appear first on the clover stems. On the surface of the agar they form in clusters so that the exuding, moist, inky-black spore masses coalesce in a rosette-like manner.

Paraffin sections. The primordium of the pycnidium arises just beneath the surface of the agar, or within the cortex of the clover stems (text fig. 10, A) and then enlarges to form a small-celled, hyaline, pseudo-

parenchymatous mass which becomes erumpent (text fig. 10, B). The cavity formation is not so distinct as in *Sphaeropsis*, evidently due to the fact that conidiophores are being formed even as the primordium increases in size. At any rate no distinct cavity filled with gelatinous substance is ever seen; instead there is a central area filled with parallel hyphae converging toward the center (text fig. 10, B). These conidiophores soon produce spores and are rapidly replaced by others which arise from the surrounding primordial tissue. The upper portions of the primordium is used for this purpose more rapidly than the lower so consequently a broad irregular ostiole is formed early (text fig. 10, C), and since the



Text fig. 10. *Hendersonia rubi* in clover stem in culture.
A Young primordium forming within tissue and disrupting cortical cells. B Later stage when cavity has formed. C Still later stage with the wide ostiole forming above. D Mature stage. The fungous tissue above has been used in spore formation, leaving an acervulus-like structure.

outer layers of the primordium have not become browned the process continues quite rapidly leaving only a basal layer, thus forming a structure which resembles an acervulus (text fig. 10, D). This same mode of development occurs in the fruit bodies that arise on the agar surface.

Discussion of the genus Hendersonia. The ability to form two types of pycnidia has been reported also for *Hendersonia piricola* Sacc. by Voges (101 and 102); only in this case he finds that the "acervulus" develops in the living leaves during the parasitic state and that the "pycnidium" arises on dead leaves and branches during the saprophytic state. He says (101, p. 92): "Womit es zusammenhängt, daß die *Hendersonia*-Pilze im Blattgewebe keine Pykniden bilden und nur im Rindengewebe, das ist schwer zu sagen. Daß hierbei ungleiche Ernährungs- und im Zusammenhange damit Wachstumsverhältnisse eine Rolle spielen,

das ist anzunehmen. Aber was für welche? Die parasitische Lebensweise im Blatte und die saprophytische in der Zweigrinde, die gar nicht so scharf auseinanderzuhalten sind, von dieser verschiedenen Ernährungsweise kann die formative Tendenz im Pilzorganismus bei seiner Fruchtlagerbildung schwerlich einzig und allein abhängen." The answer to this question raised by Voges regarding the cause of the presumptive dimorphism of *Hendersonia* is to be obtained by comparison with developmental histories of pycnidia produced in culture by other species, i. e. *Septoria* (p. 15) and *Phomopsis* (p. 19). Under these two species there has been presented a discussion of the browning or oxidizing concerned in the formation of pycnidia; so in like manner the same explanation applies to *Hendersonia*. Evidently the combination of environmental factors, whatever they may be, necessary for this oxidizing are not present during the parasitic state of *H. piricola* nor in the pure cultures of *H. rubi* but they do seem to function under the saprophytic conditions in the case of *H. piricola* and of *H. rubi* at certain places on branches with loosened epidermis. In living leaves and artificial cultures the growth conditions were favorable, pycnidial development was rapid, plenty of moisture was present, no browning took place, therefore an acervulus resulted; while under saprophytic conditions during the winter, growth was slow, perhaps the moisture content of the particular substratum was low, browning took place, and therefore a pycnidium resulted.

It is quite likely that still other species of Hendersonia react in the same manner although nothing to this effect has been found in the literature. Wolf (109, p. 128—129, figs. 6—8) describes and illustrates for *H. opuntiae* E. & E. a typical pycnidium and he mentions the production of fruit bodies in culture but says nothing of their structure there. Zeller (110) in his studies with *Coryneum ruborum* Oud. illustrates a mature, and therefore, acervulus-like fruit body (which resembles the structure given by me for *H. rubi* in text fig. 9, A) but he does not mention any other pycnidial form.

Although one can not make positive statements based merely on the examination of exsiccati yet there are several species which give evidence of behavior similar to that reported for *H. piricola* and *H. rubi*. *Hendersonia celtifolia* Cooke, in Ellis N. Amer. Fungi no. 1174, shows a globose pycnidium but with an extremely delicate, hyaline wall. *H. rosae* Kickx, Sydow Myc. germ. no. 420; *H. vitis* Died., Sydow Myc. germ. no. 1372; *H. rubi* (West.) Sacc., Sydow Myc. germ. no. 1701; *H. rubi* (West.) Sacc. var. *rubi idaei* Brun., Sydow Myc. germ. no. 1702; and *H. peckii* Clinton, Ellis N. Amer. Fungi no. 414 all have fruiting structures identical with that given in text fig. 9, A. On the other hand there are *H. sarmentorum* West. var. *sambuci* Sacc., Sydow Myc. germ. no. 338; *H. hirta* (Fr. p. p.) Curr., Sydow Myc. germ. no. 2192; and *H. phragmites* Desm., Sydow Myc. germ. no. 1700 which have definite globose pycnidia with a definite browned

enveloping layer as illustrated in text fig. 9, E. Whether or not these several species are capable of forming the two types of fruit bodies can be determined, of course, only by careful cultural and observational methods; yet judging from the fact that from two to five species of *Hendersonia* are reported on the same host plant in a large number of cases, it would seem likely that at least some of the so-called species are nothing more than different stages of the same fungus. This is especially probable where one species is described with "depressed pycnidium" and another with "globose pycnidium, as in the case, respectively, of the following pairs of species: *H. syringaecola* Brun. and *H. syringicola* Brun.; *H. piricola* Sacc. and *H. mali* Thüm.; *H. malvacei* Brun. and *H. grossulariae* Oudem.; *H. henriquesiana* Sacc. & Roum. and *H. canina* P. Brun.

In this matter of a fruit body that appears at first as a pycnidium but which finally resembles an acervulus, there are two other genera in which the same thing occurs. They are *Asterosporium*, reported by the writer in a previous paper (3), and *Pestalozzia* (p. 66). As a matter of fact *H. rubi* resembles the two species of *Pestalozzia* a great deal, both in cultural characters and morphology. Whether or not such forms will warrant a separate division in a systematic presentation can only be determined by the investigation of other related genera, especially some species of *Gloeosporium* and representatives of the *Leptostromaceae.*

Voges (101, p. 90) has already pointed out that *H. piricola* should belong to a genus near *Coryneum.* There are species described under *Coryneum* which clearly are nothing more than false species. In the first place the original description of *C. ruborum* Oud. (in Saccardo's Sylloge) together with the additional description and illustration by Zeller (110), when compared with the writer's collection and with *Hendersonia rubi* (West.) Sacc. and *H. rubi* (West.) Sacc. var. *rubi idaei* Brun. in Sydow Myc. germ. nos. 1701 and 1702 respectively, indicate complete agreement even to minute details. The conidiophores with broadened bases as reported by Zeller (l. c.) are to be found in both *H. rubi* and the variety *rubi idaei.* In structure, the fruit bodies of both species are indistinguishable from the description given for that of *H. rubi.* In like manner the original description of *Hendersonia platypus* E. & E. (cf. Saccardo's Sylloge) quite evidently applies to the fungus in question. The synonymy of the fungus on *Rubus* as a result of this investigation stands as follows:

Hendersonia rubi (West.) Sacc.

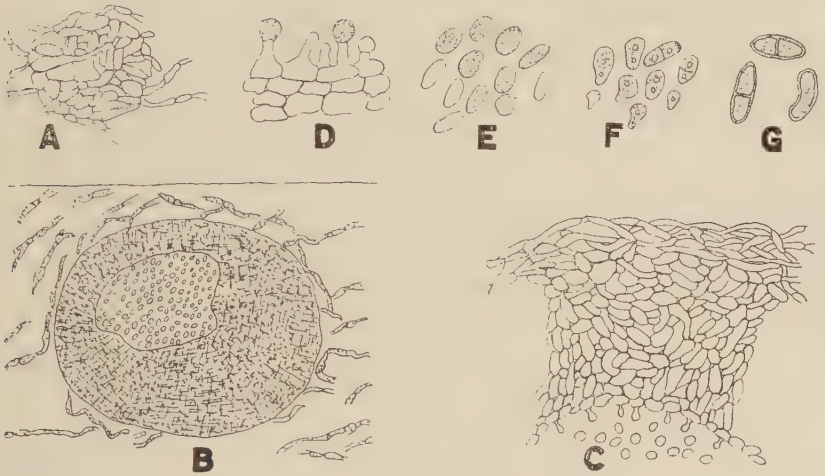
H. sarmentorum West.
H. rubi (West.) Sacc. var. *rubi idaei* Brun.
H. platypus E. & E.
Coryneum ruborum Oud.

In addition it would seem that such heterogeneous species as *Coryneum microstictum* Berk. & Br. and *Coryneum foliicolum* Fuckel might also be considered as synonyms, at least in so far as they are reported on *Rubus.*

Undoubtedly there is difficulty in separating the genera *Coryneum* and *Hendersonia*, especially in respect to some species, and yet an examination of the exsiccati of *Coryneum disciforme* Kze., in Ellis N. Amer. Fungi no. 1378; *C. kunzei* Cda. in Ellis N. Amer. Fungi no. 632; and *C. negundinis* E. & E., in Ellis & Ev. N. Amer. Fungi no. 3562 shows that there is a distinctly different type of fruit body in these cases. The spores arise not in a cavity but from the upper surface of a convex basal layer, evidently in much the same manner as in *Vermicularia* (p. 67).

Coniothyrium concentricum (Desm.) Sacc.

On the host. The fruit bodies on living leaves, arise within a roundish zone of dead tissue which is delimited by a brown, elevated rim. The



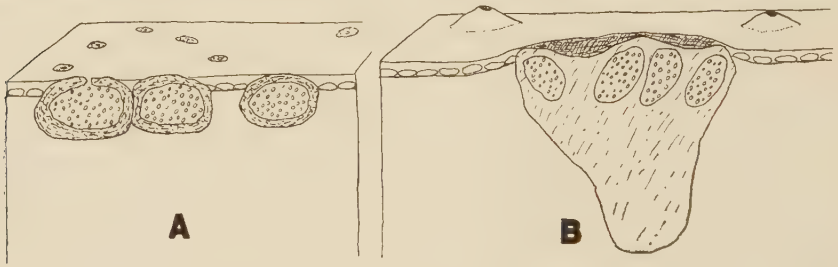
Text fig. 11. *Coniothyrium concentricum* in culture.
A Young primordium in agar. B Nearly mature pycnidium embedded in agar. C Enlarged portion from B to show nature of tissue. D Portion from C to show hymenium and mode of spore formation. E Spores from culture. F Spores from Sydow exsiccati. Some are septate. G Abnormal spores occasionally found in culture.

spots are rather irregular in size and shape, often confluent and then large, appearing on both sides of the leaf; with age the cuticle becomes loosened and white-bleached. The pycnidia arise just below the epidermis and when mature the upper wall is intergrown with the epidermis (text fig. 12). Usually they are single, somewhat globose and then embedded, but quite often they are aggregated-confluent to form an irregular mass (text fig. 12, B) and then are often erumpent-superficial. The culture to be discussed subsequently was obtained from such an irregular body. The spores are brown, globose-ovoid, measure 4—6 μ, and are borne on short rod-like, hyaline conidiophores (text fig. 11, D) which line the cavity. Some of the pycnidia contain only globose spores. No definite ostiole is formed but it seems that usually there is merely a rupture or dissolution

in the upper wall, at a point just below a stoma, which allows for the discharge of the spores. Quite a number of the pycnidia are abortive, i. e. they have the same external appearance and the same structure as the normal pycnidia but instead of the usual tightly packed spore mass only a loosely woven mesh of hyaline, irregular hyphae can be found filling the cavity.

Cultural characters. The middle stratum is at first white but later brownish; the aerial is short fuzzy and greenish-gray. On agar the pycnidia tend to arise in a concentric manner and are embedded in the middle stratum. The spores ooze out in inky-black, moist masses and practically all are brown, globose, and measure 6—11 μ (text fig. 11, E), although a few oblong ones, sometimes distinctly 1-septate (text fig. 11, G), and measuring 12—20 ⩽ 6—10 μ, can be found.

Paraffin sections. In agar the pycnidia arise singly and develop from small primordia (text fig. 11, A). The cavity appears near the center



Text fig. 12. *Coniothyrium concentricum* on host.
A Separate pycnidia. B Composite fruit body.

of the primordium (text fig. 11, B) and may enlarge irregularly but eventually a fairly regular outline is formed. There was no evidence of an ostiole in the sections examined but there must be some mode of egress for the spores because otherwise there could be no explanation of the exuded spore masses seen in the cultures. Most likely there is, in the older pycnidia, a disintegration of the upper wall to form a small pore like that described on the host.

On clover stems the pycnidia are quite irregular in shape and size; the larger and most irregular ones are superficial while the smaller and more regular ones are embedded irregularly within the clover stem. All the fruit bodies in the stem cultures were sterile like those described on the host and while no valid explanation can be offered, they are probably the result of unfavorable physiological conditions.

Discussion of the species and related forms. von Höhnel (47, p. 194—195) studied *C. concentricum* and, because of certain aspects of the pycnidial structure, placed the fungus in his new genus *Dothisphaeropsis* (49, p. 82), characterized as: "Nebenfrucht von *Haplotheciella* v. H. Pykniden-

artige Lokuli, hohlig, rasig verwachsen, in der Epidermis eingewachsen, mit durch braune Hyphen angedeutetem Stroma, rundlich, mit der Epidermisaußenwand verwachsen. Ostiolum rundlich. Conidienträger kaum sichtbar. Conidien klein, einzellig, länglich oder rundlich, gefärbt."

Petrak (72, p. 2—8) incorporated *Dothisphaeropsis* into a short key, which purposed to contain the new genera derived from the mixed groups, *Coniothyrium* and *Haplosporella*. The writer offers no criticism or commendation for this particular grouping, since only one representative was studied, but there does seem to be some confusion and contradiction of terms with reference to the separations based on stroma character. Petrak (l. c. p. 6), under the heading: "Stroma fehlend oder sehr schwach entwickelt" partially characterizes the genus *Dothisphaeropsis* as: "Pyknidenmembran dick, stromatisch gebaut, ..." This use of the term stromatic alone would make the key uncertain but he adds: "Meist nur ein, seltener mehrere Lokuli vorhanden." Such a condition as the latter (cf. text fig. 12, B) is quite definitely "stromatic" in the sense of von Höhnel (see p. 75). Obviously then the separation of the genera on this one character is not tenable although most of the genera probably are valid, i. e. with the exception of *Sclerothyrium* and *Microsphaeropsis*.

The genus *Sclerothyrium* is based by von Höhnel (47, p. 181) on *Scl. tamarisci* (Mont.) v. H. as the type species, which has *Coniothyrium caespitulosum* Sacc. as a synonym. Under the genus description von Höhnel (l. c.) says: "Konidienträger fehlend. Konidien aus dem Binnengewebe endogenospor entstehend, ..." yet the writer's examination of *Coniothyrium caespitulosum* Sacc., in Sydow. Myc. germ. no. 268, shows minute though, nevertheless, definite conidiophores. A number of these Endogenosporae genera have been established and apparently they have doubtful value, especially since all have been set up merely as a result of examination of herbarium material (See also p. 10).

von Höhnel (49, p. 82) endeavors to distinguish the genus *Dothisphaeropsis* from *Microsphaeropsis*. He established the latter (46, p. 267) on the species *Coniothyrium olivaceum* Bon. but, as Petrak (72, p. 4) has pointed out, this heterogeneous species is far to uncertain for the purpose. In the key given by Petrak (l. c. p. 6) *Dothisphaeropsis* is characterized by "papillenförmig" and *Microsphaeropsis* by "stäbchenförmig" conidiophores. It has been definitely shown (text fig. 11, D) that the conidiophores of *C. concentricum* are not papilliform and thereby the distinction between the two genera falls down since the stromatic characters of the two have already been shown to be confusing and of very little importance.

The specimen issued as *Coniothyrium hysterioideum* Karst. & Har., in Briosi & Cav. no. 246, is quite evidently nothing more than a form of *Coniothyrium concentricum*. Some of the pycnidia are confluent and form such a structure as is illustrated in text fig. 12, B, while others are single and then appear like those in text fig. 12, A. The spores are not different

from those given in text fig. 11, E. Petrak and Sydow (77, p. 320—321) redescribe *C. hysterioideum* as *Microdiplodia hysterioidea* (Karst. & Har.) Petr. & Syd. and characterize it as follows: "Konidien länglich, kurz zylindrisch oder länglich eiförmig, beidendig kaum oder nur unten schwach verjüngt, stumpf abgerundet, gerade oder schwach gekrümmt, zuerst einzellig, später oft ungefähr in der Mitte mit einer Querwand, kaum eingeschnürt, ... 7,5—11 ⩽ 3—5 μ .... Pseudophysoiden zahlreich, bis über 75 μ lang, einfach oder ästig." In *Coniothyrium concentricum*, in Sydow Myc. germ. no. 139, the writer finds a specimen that corresponds to this description by Petrak in so far as the irregularity of the spore is concerned. A great majority are globose with one oil droplet but many are irregular, some are angular or oblong, and others are narrowed below; often the irregular-angular ones have two oil droplets or even a few may be 1-septate (text fig. 11, F). The "Pseudophysoiden" mentioned by Petrak are evidently comparable to the hyphae seen by the writer in culture as well as on the host. Considering these accumulated facts there is reason to consider that *C. concentricum* has rather variable spores and that the septate form seen in culture and described by Petrak and Sydow (l. c.) are abnormalities; perhaps the result of unfavorable physiological conditions. At any rate it is best to omit the name *Microdiplodia hysterioidea*. Likewise the species *C. dasylirii* Cel., *C. dehiscens* Sacc. & Speg., and *C. yuccae* Speg. should be reduced to synonomy. von Höhnel (47, p. 195) refers to *C. agaves* (Mont.) Sacc. in comparison with *C. concentricum* with the brief statement: "das Stroma entwickelt sich unter der Epidermis und die Fruchtkörper sitzen ganz oberflächlich auf den Spaltöffnungen. Der Vergleich der beiden Pilze muß zeigen, ob es sich hier nur um eine durch äußere Umstände erzeugte Wuchsform desselben Pilzes oder um einen davon verschiedenen Pilz handelt." The writer has already pointed out that both superficial and immersed fruit bodies were present on the host and this was also true of the specimen in Sydow Myc. germ. no. 139. The erumpent fruit bodies are undoubtedly merely growth forms and the several species based on this character are to be considered as synonyms. The fungus, then, should perhaps best remain in the genus *Coniothyrium* until more extensive studies are made. Following is the synonomy of the fungus based on the studies presented:

Coniothyrium concentricum (Desm.) Sacc.

Phoma concentricum Desm.
Papularia concentrica Desm.
Phoma agaves Dur. & Mont.
Coniothyrium agaves (Mont.) Sacc.
C. concentricum (Desm.) Sacc. var. *agaves* Sacc.
Coniothyrium dasylirii Celotti
Coniothyrium biforme Winter
Coniothyrium hysterioideum Karst. & Har.

Microdiplodia hysterioidea (K. & H.) Petr. & Syd.
Dothisphaeropsis concentrica (Desm.) v. H.
Coniothyrium dehiscens Sacc. & Speg.
Coniothyrium dasylirii Speg.?
Coniothyrium yuccae Speg.
Coniothyrium herbarum C. & E.

An examination of the exsiccati of other species in the *Coniothyrum-Haplosporella* group appears to lead to the following changes: *Coniothyrium herbarum* C. & E., in Ellis N. Amer. Fungi no. 1366, is nothing more than a specimen of *Kellermania anomala* (Cke.) v. H. *Haplosporella gleditschiaecola* (Cke.) E. & E., in Ellis & Ev. N. Amer. Fungi no. 3452; *H. hippocastani* E. & E., in Ellis & Ev., N. Amer. Fungi no. 2563; *H. longipes* E. & B., in Ellis & Ev. N. Amer. Fungi no. 3454; and *H. velata* E. & B., in Ellis & Ev. N. Amer. Fungi no. 3361 are merely immature *Diplodia* species and in all are found spores in various stages of septum formation. The tissue is typically that described for the *Sphaeropsis-Diplodia* group and the fruiting structure consists rather of aggregated pycnidia than of loculed stromata. The species of *Haplosporella* mentioned should be placed respectively as synonyms under the corresponding species of *Diplodia.*

C. Pachystromaceae sphaeriales, Erectae-coriaceae (Sensu von Höhnel).

Micropera caespitosa (Peck) comb. nov.

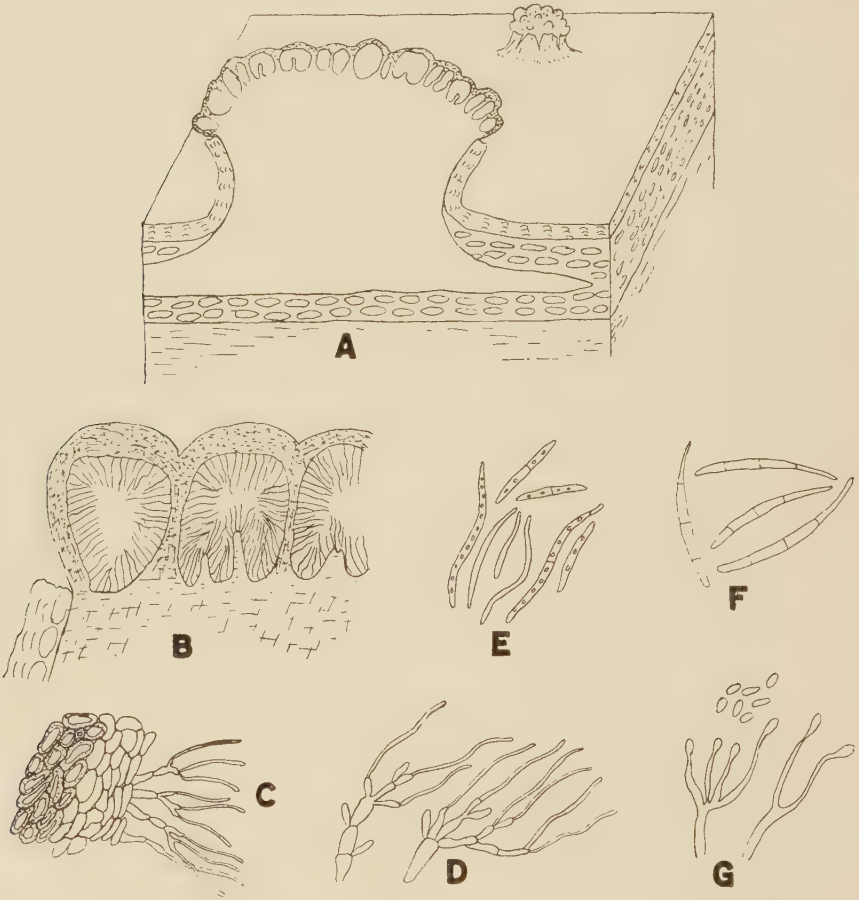
Sphaeronema caespitosum Peck
Sphaeronema stellatum Ellis
Sphaeronema peckii Sacc. & Syd.
Sphaerographium stellatum (Ell.) Sacc.
Micropera stellata (Ell.) Jacz.

On the host. The fruit bodies are blackish, erumpent and erect, verruciform and somewhat capitate-cylindrical. They arise below the thick periderm and have an effuse basal portion extending between the periderm and cortex (text fig. 13, A). The parenchyma-like tissue is rather cartilaginous and consists of cells with thickened walls. The entire tissue is light brownish but the upper, outermost layer exposed to the air is dark brown (text fig. 13, B—C). The several irregular cavities are disposed near the upper periphery and are lined with irregularly branched, septate conidiophores (text fig. 13, B—C). The spores are filiform to spindle-shaped, measuring 15—35 $\times$ 2—2,5 μ; some are obscurely 1-septate while others contain a row of large oil droplets (text fig. 13, E).

Cultural characters. The middle stratum is thin and brown; the aerial is short, collapsed and grayish-green in color. The fruit bodies form abundantly and are scattered, globose structures half-buried in the

medium and topped with a grayish mat of hyphae. The spores are rod-shaped to narrowly ovoid, hyaline, 1-celled, 3—4 ⩽ 1—2 μ, and are borne on branched conidiophores (text fig. 13, G).

Paraffin sections. On clover stems the primordia arise in groups (Pl. 6, fig. 1) within the cortical tissue and they consist of brownish hyphae



Text fig. 13. *Micropera caespitosa* on host.

A Composite fruit body with row of locules at top. B Portion from A to show darkened tissue surrounding locules. C Portion from locule in B to show detail of cells composing the tissue and the attachment of conidiophores. D Types of conidiophores. E Immature spores from writer's collection and from young pycnidia in Ellis exsiccati. F Mature spores from Ellis exsiccati. G Conidiophores and spores from culture. (Vide Plate 6.)

closely interwoven to form a tight knot. By enlargement these primordia become confluent to form an extensive mass of tissue (Pl. 6. fig. 2) which breaks apart or fills the cortical cells. Finally there appear at several points certain areas which are more deeply staining with safranin and in these the cavities arise (Pl. 6, fig. 3). The cavity is lined with the

conidiophores and the tissue immediately adjacent is reddish-stained, indicating some sort of dissolution that is taking place. Additional cavities continue to form so that finally there may be a row of seven to twelve. In older stages the walls between the separate cavities disappear leaving a single large, irregular chamber. In agar the fruit body evidently arises from a single primordium which enlarges in the manner described above and develops a single cavity.

Remarks on the species. An examination of *Sphaeronema stellatum* Ellis, in Ellis & Ev. N. Amer. Fungi no. 2170, reveals an apparently older stage of the fungus described above. Some of the pycnidia are exactly like that given in text fig. 13, A, but others are found in which the cavities have become confluent to form a single irregular chamber and in still others there seems to have been apical growth to form elongated, cone-like ostioles. The spores in the evidently older pycnidia are subfusiform, slightly curved to sigmoid, one end being more attenuated than the other, usually 3-septate, greenish-hyaline, 24—40 ⩒ 3—4 μ, and with no oil globules (text fig. 13, F). However, in some of the smaller and evidently younger pycnidia the spores are indistinguishable from those described in the writer's own collection, while in the very smallest pycnidia the spores measure 10—11 ⩒ 1—2 μ and then correspond in length to those given for *Sphaeronema caespitosum* Peck. Jaczewski (52, p. 366) examined the same exsiccati mentioned above and placed the fungus in the genus *Micropera*. He described the spores as: ". . . subfusiformes, arquées ou en forme d'S., unicellulaires, pluriguttulées, hyalines de 25—40 ⩒ 4—5 μ" and adds ". . . . l'espèce se rapproche beaucoup par l'habitus général de *Sph. caespitosum* Peck et n'en diffère que par les spores."

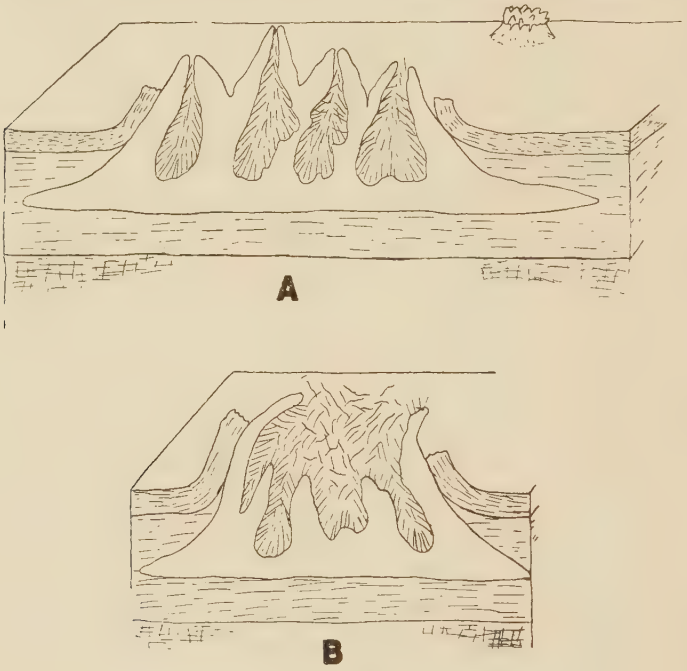
The writer considers his collection to be like the *Sphaeronema caespitosum* Peck as described by Jaczewski (l. c. p. 309) and that both are young stages of *Micropera stellata* (Ellis) Jacz. (l. c. p. 366). On the basis of this conclusion the new combination and synonomy is suggested.

The short rod-like spores obtained in culture are to be considered as the second spore form reported by Brefeld (12, p. 291—292) in the pycnidial stage of several species of *Dermatea*. He states: "Die meisten Formen bilden aber in den Pykniden neben gleichartigen Konidien noch andere, kleinere, ebenfalls meist gekrümmte, fadenförmige Sporen, deren Keimung nicht beobachtet ist. Bald herrscht in einem Fruchtkörper die eine Sporenform vor, bald die andere, bald sind beide überhaupt auf verschiedene Behälter verteilt."

Micropera drupacearum Lév.

On the host. The fruit body arises in the periderm and is strongly erumpent. The shape is quite irregular, sometimes with conical-papillate projections above, or again it may be merely verruciform (text fig. 14, A). In young stages the color is tan but changes to cinereous with age. Several

cavities arise in the upper portion of the fruit body and finally may become confluent to form a single irregularly lobed chamber, occuping the greater portion of the structure. There may be several irregular ostioles (text fig. 14, A) or a single opening, wide and gaping (text fig. 14, B). The pycnidium has an internal, yellowish or almost hyaline tissue of irregular, fused, plectenchymatous cells; an outer layer of brownish or reddish cells (the reddish discoloration some times spreading to the adjoining host tissues); and a basal portion intermixed with the disintegrated periderm cells. The spores are borne on short rod-like, rather indistinct



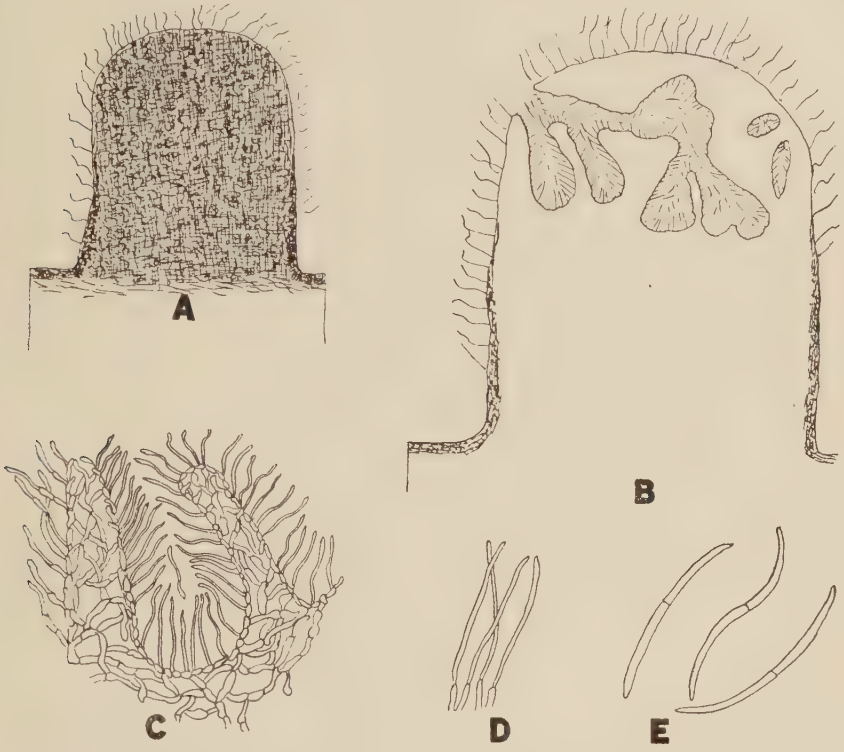
Text fig. 14. *Micropera drupacearum* on host.
A Composite pycnidium with several locules. B Ditto, showing formation of wide ostiole.
(Vide Plate 7.)

conidiophores which line the cavities; they are slender, curved, thread-like (38—60 ⩻ 2—3 μ), with pointed ends, and usually have a septation of the plasma at the center (text fig. 15, D—E).

Cultural characters. The mycelial development is slow and confined mostly to the central portion of the agar surface. The middle stratum is disc-shaped and grayish, while the submerged consists of pinkish hyphae and may cause a reddish discoloration of the medium. The fruit bodies are conical-globose and tend to arise in a concentric manner.

Paraffin sections. The development of the fruiting structure in culture is much the same as that observed on the host. On agar the early

stages of primordium were not observed but at any rate a pillar-like mass of more or less tightly woven hyphae is formed as in text fig. 15, A, which is a stage just previous to cavity formation. The cavities arise irregularly in the upper portion of the primordium (text fig. 15, B) and may soon become confluent to form a single irregular cavity with the entire surface lined by the short stalk-like conidiophores (text fig. 15, B—C) which bear the long filiform spores. In the meantime the outer



Text fig. 15. *Micropera drupacearum* in culture.
A Nearly mature primordium on agar. B Pycnidium on agar with several locules. C Portion from B to show details of one locule lined with spores, and the nature of the tissue surrounding the locule. D Conidiophores from C. E Mature 1-septate spores. (Vide Plate 7.)

layer of the structure has become browned to form an envelope above. This brown layer does not encompass the fruit body at the base but instead follows along the surface of the agar. Quite often the pycnidia, after becoming mature, rupture at the apex to form a saucer-shaped structure (Pl. 7, fig. 2).

On clover stems the story is scarcely different. The early primordial development takes place within the tissue of the stem where the developing hyphae are intercellular and gradually disrupt the cortical tissue to form a papillate protuberance. Further development results in the com-

plete upheavel of the cortical tissue and in actual dissolution of the cells. Just as in agar, several cavities arise which usually become confluent to form one chamber (Pl. 7, fig. 1). The development throughout resembles rather closely that of *Cytospora minuta* (p. 24—26).

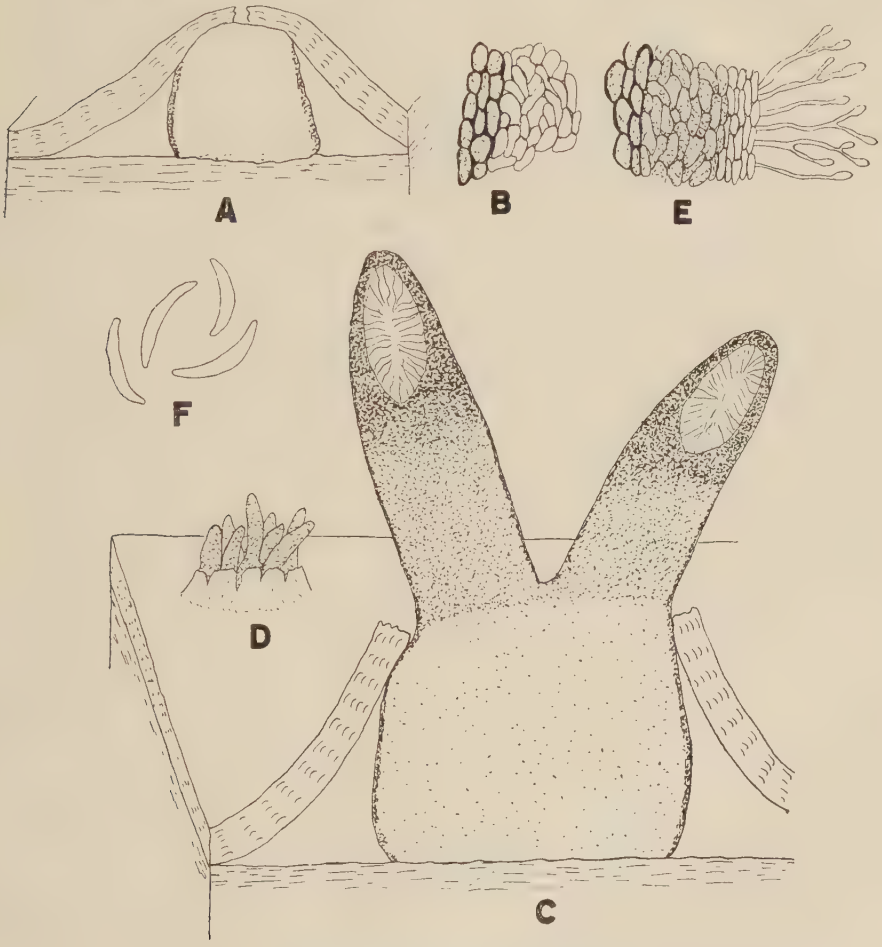
Micropera spuria (Fr.) v. H.

On the host. The grayish-black, cylindric-conic pycnidia protrude through lenticels or ruptured transverse places in the periderm to the height of about 1 mm. (text fig. 16, D.) They occur in evenly scattered groups of one to seven pycnidia, conforming in transverse alignment to the shape of the ruptured aperture through the periderm. Each group is to be considered as a number of separate pycnidia with confluent bases, as will be explained later under the description of the development of the fruit body in culture. The pycnidia arise in the cortex just beneath the thick periderm (text fig. 16, C) and the portion below the ruptured periderm is hyaline, or at least with the exception of a thin outer layer, while the portion above, in which the spore cavity develops, is light brownish. In text fig. 16, A is shown the pillar-like primordium, which is lifting the periderm preparatory to the final rupture. After the emergence of the primordium there is formed the cone-like structure in which the spore cavity develops. The tissue throughout is more or less cartilaginous, consisting of fused, hyaline plectenchymatous cells (text fig. 16, B). The ovoid spore cavity borne at the very apex in lined and quite filled with conidiophores (text fig. 16, C) which are hyaline, branched and give rise to the spores at the ends of the branches (text fig. 16, E). The spores are fusoid, with rounded ends, hyaline, slightly sickle-shaped, quite often contain irregular oil droplets or globules, and measure 10—18 $\leqslant$ 2—4 (text fig. 16, F.).

Cultural characters. The development of the mycelium is slow and the fruit bodies appear after 4 weeks. On agar the middle stratum has a yellowish-brown color; the aerial is scanty; the submerged ramifies throughout the media in delicate strands. The fruit bodies tend to form singly in a concentrical fashion. At first they are globose-conical but later there is formed at the top an elongated, creamy-yellow structure which bears the spore cavity. The spores are slightly larger in culture, measuring 14—22 $\leqslant$ 4 μ.

Paraffin sections. The story of the development of the pycnidium in culture is much the same as that already given for the fungus on the natural substratum except that here more details can be recorded. The mound-shaped primordium arises in the middle stratum of hyphae at the surface of the agar (Pl. 8, fig. 1) and consists of plectenchymatous tissue. Evidently by apical growth and elongation there is eventually formed such a structure as seen in Pl. 8, fig. 2 and the tissue in this consists of fused cells much as shown in text fig. 16, B. A mat of dark staining hyphae

at the top by proliferation gives rise to the conical structure seen in Pl. 8, fig. 3. The encircling whorl of loose hyphae indicates that the development is not entirely complete. The cells in the central area of this new tissue divide continuously to form a mass of extremely delicate



Text fig. 16. *Micropera spuria* on host.
A Pillar-like primordium beneath the periderm. B Portion of tissue from A. C Mature fruit body with locules at tip of of cone-like extensions. D Habit view of fruit body. E Portion of tissue from locule in C to show dark outer tissue and meristematic layer which gives rise to the branched conidiophores. F Types of spores. (Vide Plate 8.)

cells with minute nuclei. This change is taking place while the loose, outer hyphae are still laying down new layers of tissue so that finally one sees such a structure as represented in Pl. 8, fig. 3. In this the indistinct central area has been replaced by ingrowing conidiophores from the tissue bordering the cavity. The cavity increases in size to

leave only a thin surrounding wall of tissue so that in a culture this upper portion containing the spores appears as a yellowish sac.

The synonymy, according to the investigations of Diedicke (23, p. 289) and von Höhnel (45, p. 36) follows:

Micropera spuria (Fr.) v. H.

Ceratostomum spurium Fr.
Calicium ventricosum Achar.
Sphaeronema ventricosum (Achar.) Fr.
Sphaeronema spurium (Fr.) Sacc.

Remarks on the genus Micropera. The original description of *Sphaeromena spurium* (Fr.) Sacc. as given in Saccardo's Sylloge was not comprehensive enough to include such a structure as described in the preceding pages but Jaczewski (52, p. 311) emended the description, on the basis of several old exsiccati, to include larger spore measurements and later Diedicke (23, p. 289) made still further changes although his illustration (l. c. p. 240, fig. 16) is scarcely typical of the writer's specimen. There is mentioned in his footnotes (l. c. p. 289), however, a collection by Jaap that is typical. This he describes as "zylindrischen Fruchtkörper fast morgensternartig auf einem halbkugligen basalen Stroma sitzen, und die sich außerdem durch längere und reicher verzweigte Sporenträger von der Art unterscheidet." Finally von Höhnel (45, p. 36) redescribed the fungus and because of its structure decided that it belongs in the genus *Micropera.*

Due principally to the efforts of von Höhnel there has been a notable reduction in the confusion of species reported on *Prunus.* These now appear in the four well defined species: *Glutinium laevatum* (Fr.) Starb. (l. c. p. 28—31); *Micropera spuria* (Fr.) v. H. (l. c. p. 36); *Micropera padina* (P.-M.) Sacc. (l. c. p. 36—37); and *Micropera drupacearum* Lév. The four, judging from various descriptions, might be indistinguishable if external characters alone were relied upon because the form of the fruit bodies seems to vary somewhat. *Glutinium laevatum*, however, is easily differentiated by its rather small, oblong spores borne laterally on the cross walls of the long slender conidiophores; *Micropera drupacearum*, well represented in Ellis N. Amer. Fungi no. 40, often has a reddish color and the spores are long, filiform, and 1—3 septate. At times the other two species might be even more confusing since both have similar spores, but in *Micropera padina* (well represented in the material of Sydow Myc. germ. no. 1379, and in the illustration by Bubák 15, p. 114) the ends of the spores are pointed while in *Micropera spuria* they are rounded (see text fig. 16, F).

The genus *Micropera* seems to be reasonably well defined as attested by the three representatives in this paper but there are several genera which von Höhnel separates from this genus on rather filmsy grounds. In his key (50) *Micula* is separated on the character of the tissue and on the shape of the locule while in Saccardo's Sylloge the separation

is based on gregarious pycnidia as opposed to the occasional caespitose structures in *Micropera*. It has been demonstrated by the writer in the case of *Micropera spuria*, at least, that the caespitose habit is not inherent and it is quite certain that *Micropera padina* does not have caespitose pycnidia. The illustration and description for *Micula mougeotii* Duby given by Diedicke (23) indicates a similarity to the species of *Micropera*. In fact there is more resemblance between *Micula mougeotii* and *Micropera padina* than there is, for instance, between *Micropera padina* and *Micropera drupacearum*. Likewise there is a striking resemblance between *Micropera spuria* and *Chondropodium spina* (B. & Rav.) v. H. (45, p. 20), the two being separated principally on the difference between the respective perfect stages(1). The connection of *Chondropodium spina* (l. c. p. 46) with *Godronia* is extremely hypothetical, so perhaps it would be more logical to consider the fungus as a *Micropera*. Petrak and Sydow (76, p. 369) point out also the seeming lack of distinction between *Chondropodium* and *Mastomyces*.

The genus *Sphaerographium* according to von Höhnel (44, p. 102), has one species, i. e. *S. squarrosum* (Riees.) Sacc. and in his key (50) it stands next to *Micula*. The statement by von Höhnel (45, p. 47) that *Cornularia hispidula* (Ell.) Sacc. belongs to *Sphaerographium* is evidently an oversight because he had previously (44, p. 117) stated that the species was a typical *Pseudographium* which agrees with the statement of Jaczewski (52, p. 374). Nevertheless an examination of the material in Ellis N. Amer. Fungi no. 113, *Cornularia hispidula* shows that there is close resemblance to the other species of *Pseudographium* but yet the genus does not differ enough morphologically to warrant its wide separation from *Sphaerographium*. The von Höhnel "*Pseudographieen*" (50, p. 307) and the "*Erectae-Carnosae*" group of the "*Pachystromaceae*" (l. c. p. 309) are separated on stromatic characters but this is not a reliable factor as will be seen in the discussion later (p. 73).

Much emphasis is placed by von Höhnel upon the connection of many species, in the "*Erectae-Carnosae*" group, with the perfect stage as a basis for separation into genera but in most cases this connection is merely inferential and is not to be relied upon too strongly. Furthermore the state of confusion among the *Ascomycetes* closely parallels that of the imperfects. Again, the group of ascomycetes, i. e. *Dermatea*, *Dermatella*, *Crumenula*, *Godronia*, *Tympanis*, *Cenangium*, *Cenangella*, etc. to which these species belong are quite similar, so it would not be surprising to find the imperfect stages to be similar also. With this state of affairs it would seem advisable to approach the matter from another angle, namely to germinate the ascopores in order to obtain the imperfect stage. This would at least form the basis for relationships, a matter that can not be decided merely by observation.

(1) *Chondropodium spina* has been carefully studied by the writer but the cultures became contaminated so that it was impossible to prepare a description for this paper.

Naemosphaeria acerina (Pk.) v. H.

On the host. Careful examination of sectioned material from the writer's collection and from Ellis N. Amer. Fungi no. 957 indicates that there is nothing to add to the excellent description given by von Höhnel (45, p. 47—49). It was found, however, that the hair-like paraphyses often were attached to the conidiophores (text fig. 17, D). Some idea of the pycnidial structure is conveyed by text fig. 17, E. The recent illustration given by Overholts (68, Pl. 10, fig. 2) is somewhat misleading because the beak of the pycnidium is curved to one side while normally it should be more erect.

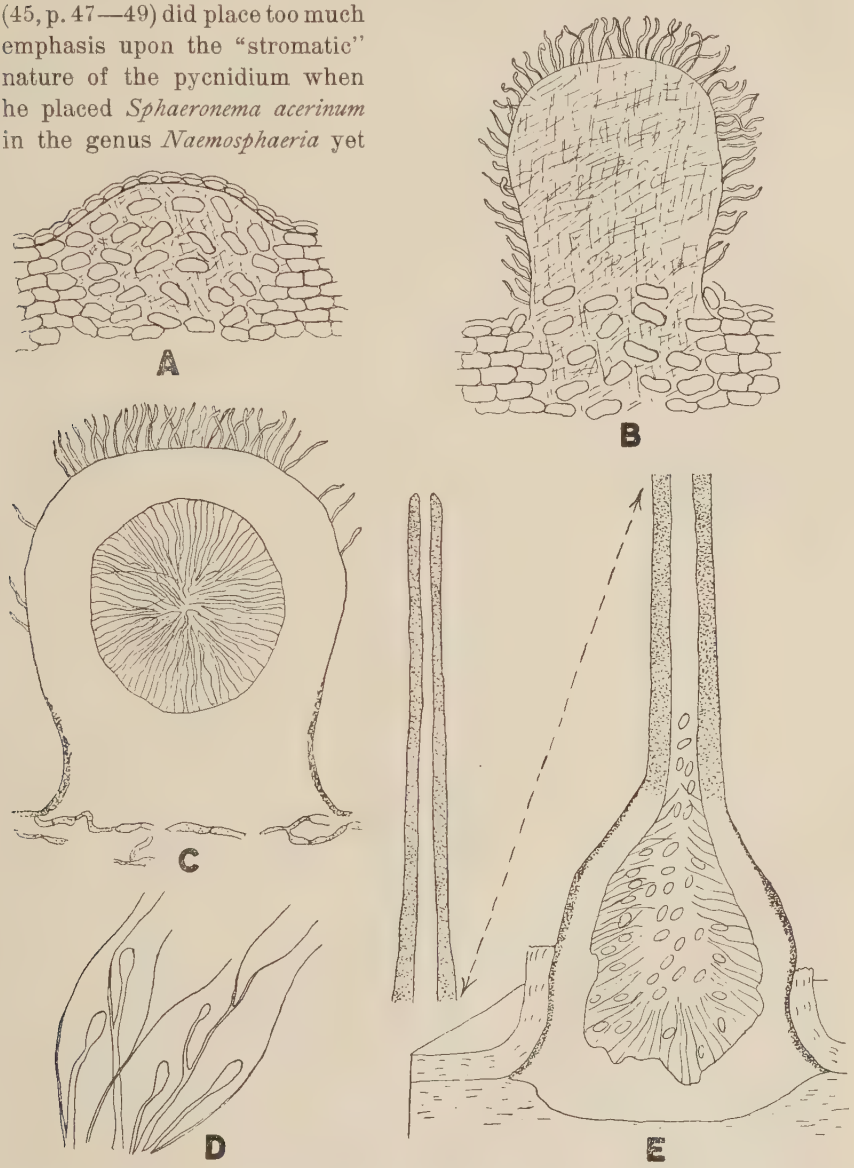
Cultural characters. The mycelial development is slow and localized, forming a grayish-brown disc at the center of the agar surface. The medium is discolored a reddish-brown. The pycnidia arise sparsely both on the media and the clover stems and the beak-like ostioles found in nature occur only in old cultures which have dried out considerably.

Paraffin sections. The primordium on clover stems arises within the cortical tissue where it disrupts the cells and produces a protuberance such as is given in text fig. 17, A. At this time the primordium consists of thin, irregularly knarled hyphae. As the primordium increases in size it becomes erumpent and finally breaks through the cuticle to form a more or less cylindrical mass of tissue (text fig. 17, B) with intermixed, loosened and partially dissolved cortical cells at the base. This structure, composed of distinct, parenchyma-like cells, enlarges by the proliferation of peripheral hyphae to form a larger structure as seen in text fig. 17, C. In this mature structure the outer layers of tissue become brown to form an enclosing brown layer along the sides. At the top, however, there is still found a weft of hyphae. It seems that a centrally located area, involving a considerable portion of the primordium, undergoes cell division to form a mass of extremely small, thin-walled, poorly staining cells; this last giving evidence of a gelatinizing process. This mass of cells is displaced by a dense formation of radially converging, hyaline filaments arising from the periphery to fill the entire cavity and by the use of the oil immersion lens it is possible to determine that the spores arise near the base of these filaments. As the pycnidium becomes more mature most of the filaments disappear leaving an almost solid mass of gelatinous substance which fills the interstices between the spores. This substance has been also observed in sectioned material from the host.

The long, slender beak ordinarily found on the pycnidium in nature was not obtained in the material cultured for paraffin sections, probably because of the presence of too much moisture. Judging from young stages seen on the original substratum and tendencies of some of the older pycnidia in paraffin sections to form masses of erect hyphae at the apex (text fig. 17, C) it seems clear that the beak arises as a result of

apical growth of the pycnidium in much the same manner as reported by Bauke (6) for the fungus called *Pycnis Pleospora polytrichia.*

Remarks on the genus Sphaeromema. Even though von Höhnel (45, p. 47—49) did place too much emphasis upon the "stromatic" nature of the pycnidium when he placed *Sphaeronema acerinum* in the genus *Naemosphaeria* yet



Text fig. 17. *Naemosphaeria acerina.*
A Young primordium in clover stem in culture. The cortical cells are being disrupted. B Primordium in culture on clover stem just before cavity formation. The encircling row of outer hyphae indicates the peripheral accretion of new tissue. C Pycnidium with cavity. The weft of parallel standing hyphae at the top indicates the manner in which the long slender beak arises. D Branched conidiophores with hair-like appendages. E Mature pycnidium from host.

it is not likely that this will impair the validity of that genus when considered from the proper viewpoint of stroma interpretation (cf. p. 73). von Höhnel (46, p. 272—284) transferred many of the species of the genus *Sphaeronema* into other genera and suggested that the remainder of the species need careful examination. This is a commendable step in an effort to untangle the confusion which exists among the various dissimilar species of the old genus *Sphaeronema;* it has been corroborated by the writer's examination of various exsiccati. von Höhnel (l. c. p. 272) considered *Sphaeronema subulatum* Fr. to be the type of the genus *Sphaeronema,* basing his decision on a list first published by Fries but Petrak and Sydow (67, p. 363) question this decision because of the fact that Fries later published another list with this species placed in a subgenus though they admit that it is difficult to decide from the writings of Fries just what the type ought to be. Undoubtedly von Höhnel also realized this truth and therefore arbitrarily chose the species in question as the type. This quibbling over what should be or should not be the type of a genus, especially in cases where the original material and description is unsatisfactory, is a matter to be decried and Shear (84) has aptly pointed out that a genus should be a vehicle for the identification of species and not for historical research.

D. Melanconiaceae.

Pestalozzia guepini Desm.

Cultural characters. The middle stratum is at first scanty and white changing to brownish-white, and consists of a very tenacious mycelium; the aerial is scant and fuzzy; the submerged is composed of delicate, hyaline strands. The medium is discolored to a canary-yellow. The pycnidia arise abundantly in more or less radiating lines and the exuding, inky-black, spore masses sometimes become confluent to form a continuous layer over the agar surface.

Paraffin sections. The primordia are superficial, at least on agar, and have a pseudoparenchymatous tissue. There is no darkened outer layer formed; a true pycnidium is developed at first, but later the entire upper portion is dissolved away leaving only a basal dish-shaped structure, the acervulus. Cavity formation is typically like that of *Sphaeropsis,* in that there is a central area dissolved out to form a small cavity surrounded on all sides by ingrowing conidiophores which soon produce spores to fill the cavity tightly. As this first crop of spores matures another layer arises below and so the process continues until all the upper tissue of the primordium is exhausted. Thereafter spore production is augmented by the proliferation of the basal layer. The mature structures measure 100—150 μ in diameter.

Pestalozzia palmarum Cooke.

Cultural characters. In culture this fungus differs distinctly from *P. guepini* in that the middle stratum remains white with the exception of a tinge of buff at the margins, in that the medium is not discolored, and in that the fruit bodies are not so abundant, but are massed together in a few clumps. Furthermore the pycnidia are larger, measuring 150—250 μ diameter and are mostly embedded in the medium.

Discussion of the genus Pestalozzia. The results obtained with these two species merely substantiate the work of Leininger (58), Bainier and Sartory (4), and Kempton (55, p. 245—247) all of whom obtained similar results although they worked with different species and culture media. Possibly the acervulus in other species of the *Melanconiaceae* is similarly developed, as already shown for *Asterosporium hoffmanni* by the writer (3). This mode of formation differs somewhat from that of a regular acervulus as produced in *Vermicularia* (p. 67).

It has been previously pointed out for *Septoria* (p. 15) that the darkening of the outer layer of the primordium is an important factor in pycnidial development in so much that the differentiated, browned outer layer, if not available for spore-formation, remains in place and thus gives the characteristic shape to the pycnidium. As to what the ultimate cause might be in this change we can advance only suppositions. Most likely the fungus produces some substance that is oxidized upon exposure to air. Since the *Pestalozzia* pycnidium does not produce this substance there is no browning; therefore the tissue is used up and an acervulus results.

Although the two species of *Pestalozzia* studied were clearly different, it may be pointed out that in Sumatra La Rue and Bartlett (57a) found that types growing on palms were not separable from *P. guepini.*

Vermicularia circinans Berk.

Cultural characters. The middle stratum is greenish at the center and white at the margins, later becoming black; the aerial is fluffy and white, appearing first at the center of the colony; the submerged is dark brown, penetrating through the medium. Sometimes there are reddish patches formed on the surface of the colony. The fruit bodies arise scattered uniformly over the media after six days but on the stems they are clustered more closely.

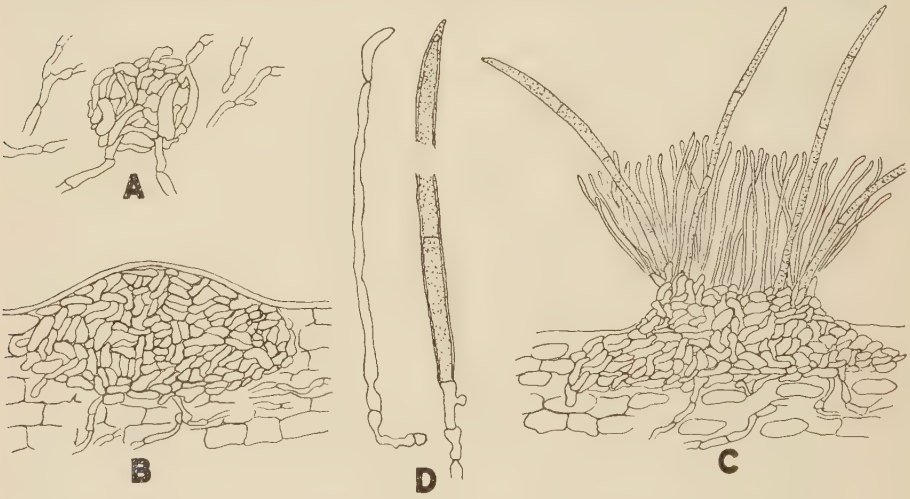
Paraffin sections. The young primordium is a small cluster of cells, arising either symphogenously or meristogenously (text fig. 18, A) below the agar surface and increasing in size so that finally the upper half is superficial. The primordium is then seen to consist of closely packed brown cells.

On agar no spores or setae were formed, at least during the first six days. The development on clover stems is similar except that the primordium remains covered by the cuticle until the formation of conidio-

phores and setae (text fig. 18, B). The conidiophores and setae (text fig. 18, D) are evidently homologous in origin since both are formed by the elongation of hyaline cells occupying a central position in the upper part of the primordium. It is the proliferation of this hyaline area that results in the fan-shaped appearance of the mature structure (text fig. 18, C). The conidiophores are hyaline and bear a single spore at the tip. The setae are heavy walled, dark brown and have several cross walls.

Vermicularia peckii Sacc.

In cultural characters this species differs only slightly from *V. circinans*, the main difference being the absence of the reddish discoloration and



Text fig. 18. *Vermicularia circinans* in culture.
A Young primordium in agar. B Nearly mature primordium on clover stem. C Mature fruit body on clover stem. D Conidiophore (right) with spore and brown seta (left), from fruit body in C.

in the variation of the fruiting process. *V. peckii* forms no acervuli on agar and only a few on stems, although the structure and development of these were like those described for *V. circinans.*

Discussion of the genus Vermicularia. von Höhnel (41, p. 442) states that Fuckel endeavored to show that the fruiting structure of *Vermicularia* was not a pycnidium and that the fungus belonged in the *Tuberculariaceae* and to this von Höhnel himself accedes by changing the entire genus to the *Tuberculariae dematieae.*

There seems to be uncertainty in the interpretation of the fruiting structure by various investigators and consequently certain of the better studied species have been shifted from one genus to another. Stevens and True (92) in studying *Vermicularia circinans* arrived at the following conclusion: "The structure is a tubercle with a differentiated cortical outer

layer. The outer layer ruptures and the tubercle develops as a sporodochium". They also describe the setae as arising from a subiculum and place the fungus in the genus *Volutella*. Kempton (55, p. 249) studied the same species and describes the fruiting structure as a black stroma-like mass of interwoven hyphae formed symphogenously from which later the sporodochium develops. Then he says that *Volutella* is distinguishable from *Colletotrichum* and *Gloeosporium* by ". . . . the formation of a more compact and usually large base or subicule upon which the sporodochium is produced". Walker (103) gives careful consideration to the viewpoint of previous investigators in relation to the structures and classification of the fungus on onion and finally concludes that the genus *Colletotrichum* is the proper place for it. He interprets the structure as a basal subcuticular stroma with a superficial acervulus.

As long as there is such a variety of interpretations of the fruiting structure there can be no uniformity of classification. From the study of the morphology of the two species in this paper compared with the descriptions and illustrations of various species and with a number of exsiccati there seems to be no good reason for retaining the genus *Vermicularia* as separate from *Colletotrichum*. The greenish color of the middle stratum and the reddish discoloration have been reported for various species by Shear and Wood (89, p. 63) and Stoneman (95, p. 73, 75, 78, 88, 89, 110). As a matter of fact Saccardo (80) infers that the group is "Genus ulterius explorandum; .... et tunc ad *Colletotrichum* vel Excipules vergentes". An examination of the literature will indicate clearly the difficulty of indentifying a species of the genus *Vermicularia* with any degree of certainity. In the first place the descriptions of various species are so much alike that practically the only difference lies in the substrata and unfortunately the matter does not end here because there are several species, i. e. *V. dematium* (Pers.) Fr., *V. liliacearum* Schw. and *V. herbarum* (Pers.) Fr., which involve dozens of host plants. Such a condition makes the identification of a fungus merely a hit or miss method. In the literature there exist descriptions of four species belonging to as many genera, i. e. *Vermicularia peckii* Sacc., *Phyllosticta trillii* E. & E., *Gloeosporium trillii* E. & E., and *Colletotrichum trillii* Tehon (99); all of them occuring on the leaves of *Trillium*. Of course there can be no assurance that the four descriptions apply to one fungus but the wording of the descriptions would make a difficult task of distinguishing between the four species, especially if we take into consideration the fact that the length of spore, the presence of setae, and the size of acervulus are quite variable. Walker (103, p. 689) mentions the effect of moisture on stroma size, while Shear and Wood (89, p. 64) indicate the variability of the setae, stating that: "Setae are frequently entirely wanting in some cultures while abundant in others from the same host. Some acervuli from one single spore culture may show many setae, others few, and still others

none." Such confusion signifies that in order to determine real species there must be more culture work and cross-inoculations of the nature already produced by Gardner (30), and Shear and Wood (l. c.). A large number, perhaps all, of the species are parasitic so that is should be possible to carry out the necessary inoculations. As parasites the fungi are most likely to be sought under the genera *Phyllosticta*, and *Gloeosporium* when occuring on leaves, and as saprophytes under the genera *Vermicularia*, *Colletotrichum*, and *Volutella*, when growing on the stems, leaves, fruits, etc.

General Conclusions and Summary.

If our classification of fungi is to be based upon the fruiting bodies it behooves us to know something about the development of these structures. It is not enough to observe merely the mature and usually dried out specimen if we hope to make the correct interpretation from the systematic standpoint. Even if we could be certain that a particular specimen was really mature the matter would yet be insecure; too often there have been misleading remarks and descriptions based upon some poorly or abnormally developed specimen. To be more confident of our ground we must know the complete development of the fungi. With this in mind it may be permissible to make a few generalizations from the all too scanty data presented in the preceding pages.

Primordia. In the few examples given us by scattered investigators we know that the higher fungi, the Basidiomycetes and Ascomycetes all have an initial stage consisting rather uniformly of an undifferentiated, more or less globose mass of fungous tissue called the primordium. All evidence points to the conclusion that this stage has an important influence on the development of the full-grown structure, to which we apply generally the term fruit body. In the Fungi Imperfecti a dividing line would fall somewhere between the *Sphaeropsidales* and the *Hyphomycetes*. More correctly speaking the line would most likely divide the *Melanconiaceae* into two groups; one with a distinct primordium and the other without such a stage. The line would not be a sharp divison it is true, for there would be species on the dividing line, a thing to be expected of all such attempts to fit living things into a man-made scheme of classification.

In the *Hyphomycetes*, it is very probable that those genera forming spores in distinct sporodochia do not possess a true fungous tissue. Even though the structure may strongly resemble that of some of the *Sphaeropsidales* yet close examination will show that the hyphae are aggregated perhaps but not fused. Among the *Melanconiaceae* we should expect to find some forms having structures composed partly of typical fungous tissue and partly of merely aggregated hyphae and to all appearances we find such forms in the *Patellina* studied and illustrated by Kempton (55, p. 247—248, fig. 117—119). The primordium of a true pycnidium is

more prone to be globose in shape and its enlargment is centric rather than excentric. The primordia of true pycnidia actually retain a somewhat globose shape up to the very time of cavity formation.

Pycnidia. The concluding statement of the preceeding paragraph is, of course, used only in a relative sense for many factors enter in to induce variations in the ultimate shape of the mature structure, for example when several primordia become confluent, or when the development is hampered or modified by the presence of a substratum or by other environmental factors. For the sake of clarity let us consider first a typical pycnidium; like that of *Sphaeropsis conspersa* (p. 31) already dealt with. Using this as the central type it is possible to consider all other known forms of pycnidia as variations of this type form. *Botryodiplodia (Sphaeropsis)* is clearly a case of several fused "*Sphaeropsis*" primordia. *Cystospora* and *Phomopsis* also have fused primordia but the fruit bodies never become erumpent. The enlargement of the young structure is due in part to external addition of new layers of tissues which, intermingling with partially disorganized cortical cells, obscure the outline of the fruit body so that there is no definite brown outer layer formed. *Septoria* forms a normal primordium at first but evidently the rate of growth of the periphery is greater than that of the interior; so that there is formed a hollow sphere with a thin wall, which is easily ruptured by pressure of the spore mass to form the wide gaping ostiole. *Pestalozzia*, although ordinarily considered as a representative of the *Melanconiaceae*, forms a normal pycnidium but has a thin wall, which, like *Septoria*, is soon broken down to form the acervulus-like base. Both *Micropera spuria* and *Naemosphaeria acerina* have normal primordia but after a certain period of development apical proliferation occurs to form the tissue in which the cavity will develop, thus resulting in a stalked structure. *Vermicularia* might be considered a type related to *Micropera* for it too has a normal primordium with apical development except that here no peripheral tissue is produced but instead spores are formed directly. *Hendersonia* and *Ascochyta* in culture form normal pycnidia but in nature, under certain parasitic conditions, the pycnidial walls remain hyaline and often indistinct so that these two, together with several other genera, have been considered by several workers as pseudopycnidial forms.

Pseudopycnidia. The term, pseudopycnidium, originally proposed by Potebnia (78, p. 58) as the result of an evident misconception of the mode of pycnidial development in *Septoria*, was applied later to other forms merely because of their morphological resemblance to the original *Septoria* and not necessarily because of similarity in the mode of development. Thus the term is doubly wrong. Two species of *Septoria* are known positively to form true pycnidia and the characteristic mode of ostiole formation observed in culture fits well with illustrations of other species and there is good reason to believe that proper investigation will reveal

a similar mode of development for other representatives of the genus. Voges (102, p. 44) has already criticized this definition of psendopycnidium yet von Höhnel (50, p. 306) has seen fit to retain the application of the term. He states: "Bei sehr kleinen, zarthäutigen Formen beginnt die Konidienbildung oft schon vor der Ausbildung des Gehäuses, das dann pseudopycnidial genannt wird *(Septoria, Ascochyta).*" Just how von Höhnel obtained this idea is unknown but at any rate the *Septoria* and *Ascochyta* species studied in this paper certainly did not form spores before the development of the pycnidium. As to the hyaline, indistinct pycnidial walls, which have led several taxonomists astray, there is yet much to be learned regarding the conditions or causes of the browning process. All the species in culture gave evidence of attaining at least partial browning and the data presented from various sources leads to the theory that it is somehow due to oxidation.

Coloration. Although no attempt has been made to find support in the literature for the writer's position yet data gathered from various sources and from study of various fruiting structures make it apparent that the browning which occurs in the tissues and spores of a large number of fungi is an oxidation process. Throughout the literature there are observations to the effect that usually those outer portions of the pycnidium exposed to the air turn brown and the same thing was observed in the fungi discussed in this paper, both on the natural substratum and in culture. In culture the structure uniformly developed a brown layer on the outside, despite the fact that in the original substratum there might be no sign of this coloration. The explanation offered for this difference is that the fruit body in culture is not shut off from contact with the air as it is when growing beneath the epidermis or within the cortex. The subject of pigmentation in fungi is far too comprehensive to be considered to any extent here except to point out that Milburn (65) and Bessey (8) have shown that the presence or absence of color depends upon environmental conditions, while Nordhausen (66, p. 16) has advanced the idea that the browning is due, in part at least, to an enzyme. de Bary (5, p. 9) has stated that: "The coloration of the membrane is accompanied with increased firmness ..... With the coloration therefore we may also speak of the sclerosis of the membranes." For our purpose, however, there should be stressed the important influence of the brown outer envelope upon the shape of the pycnidium. Vestergren (100, p. 4) considers this outer layer to be composed of dead cells. At any rate we are certain that, once becoming browned, the tissue remains practically unchanged; although the inner hyaline tissues may disappear entirely, due to the transformation wrought by cavity development and spore production.

Cavity formation. The steps which precede cavity formation are similar in practically all the forms studied. The primordial cells undergo

division to form a mass of deeply staining tissue. Coinciding with this change there is usually a dissolving or lysigenetic action in a portion of the newly formed tissue to produce a gelatinous substance which may persist for a time after the beginning of spore formation. In none of the forms studied was there found anything comparable to the schizogenetic mode of cavity formation discussed by de Bary (5), Dodge (24) and others.

It is from the cells facing into the cavity that the spores arise and, typically, there is first formed a conidophore which by enlargement at the upper end develops into the spore. We have seen, however, in some genera that the spores arise directly from the primordial cell, i. e. without any intervening conidiophore. The two forms are not fundamentally different since a spore is to be considered merely as the extruded contents of the primordial cell. Spore formation, the shape, the absence or presence of color and of septation in a spore are fairly constant characters for any one species, although the two last named are sometimes delayed, under circumstances not well understood, and then lead to confusion in taxonomic keys. This confusion has been aggravated by the fact that delayed coloration does not seem to interfere with the germination of the spores in some species. The common assumption has been that germination was a sign of maturity. For spores formed within sexually induced organs there is good reason for the idea that ability to germinate is coincident with maturity. The same reason however, does not apply to pycnidiospores. The facts lead us to believe that the hyaline and the brown-walled spores of a species of this group are fundamentally the same with respect to maturity. It is often true, for example, in species of *Sphaeropsis*, that the hyaline spore will germinate more readily than the brown one. de Bary (5 p. 9) reports that "the coloration of the membrane is accompanied with increased firmness and in most cases with exceptional power of resisting the action of concentrated sulphuric acid" while Bauke (6), in speaking of spore germination in a *Diplodia*, says that the heavy brown exospore is shattered by the exit of the germ tube, and Wenner (107, p. 377) says the same of *Pestalozzia*. It is often possible to crush the spores in such a manner as to cause the heavy brown covering to be cracked free from the hyaline inner portion. These facts would imply that the brown exospore in reality acts as a hindrance to the germination of the spore, since the germ tube must exert sufficient force to burst through the heavy membrane. The data presented for spore germination in *Asterosporium hoffmanni* by the writer (3, p. 227—228) also bear out this conclusion.

Stroma. Perhaps the most misused and confusing term is stroma. There is scarcely a single paper dealing with the morphology of pycnidia in which the term has not been used in a loose and often incorrect sense. The origin of the term "stroma", its early usage and its later application, especially in the Ascomycetes, has already been dealt with thoroughly by Orton (67) but so far no one has commented on the general misuse

of the term as applied to the fruit bodies of the *Sphaeropsidales*. Apparently this misuse has been due to two reasons; first, that heretofore there have been no careful comparative morphological studies based on a large number of types; and second, that there is a similarity in structural morphology between the sexually-produced perithecia of the Ascomycetes and related imperfect forms. With reference to the last there have been many intimations scattered throughout the literature, i. e. Brefeld (12, p. 245), Ruhland (79, p. 47), Bauke (6, p. 323) etc., remarking on this similarity. That there has been a loose usage of the term stroma among the Ascomycetes is evident, but the scope of this paper does not allow for discussion of that phase and, moreover, Orton (67) has already dealt with the subject comprehensively, and recently Wehmeyer (106) has offered a new definition of the term in the light of his observations on the morphology of the *Sphaeriales*.

From the studies presented in this paper the writer defines stroma as: all the fungous tissue which surrounds the cavity or cavities in a closed fruit body or which lies under the hymenial layer in an open fruit body. Before cavity formation or spore origin the stroma and the primordium are equivalent terms, at least from a morphological standpoint. In the mature fruit body we may say that the stroma is any and all primordial tissue which has not been or which is not being transformed into spores. This is true whether the fruit body contains one regular cavity, as in *Phoma;* or one large irregular cavity, as in several species of *Cytospora;* or several separate cavities, as in *Dothiorella*. It has been shown that genera ordinarily considered as non-stromatic, i. e. *Phoma*, *Sphaeropsis*, *Ascochyta*, *Diplodia* and *Septoria* are forms with simple, 1-loculed pycnidia which arise from a single primordium. On the other hand, genera ordinarily considered stromatic, i. e. *Cytospora*, *Phomopsis* and *Botryodiplodia*, are forms with composite, many-loculed pycnidia which arise from several confluent primordia. Before any further consideration of the concept "stroma", it might be well to consider the usage of the term as it has appeared in the literature with reference to the *Sphaeropsidales*.

Bauke (6) in his introduction criticizes the Tulasne definition of conidia, "as free-forming on a stroma or hyphae", and of stylospores, "as borne within closed bodies", by pointing out that often the stroma which bears conidia may have an irregular surface or deep depressions thereby approaching the closed cavity. However, he finally adds that when a definite cavity is formed, the structure should then be known as a pycnidium but he does not attempt any further distinction of stroma. Lindau (62, p. 347) states that the stroma as opposed to the subiculum ". . . repräsentiert festere Gewebekörper, die den gleichbenannten vegetativen Gebilden der stromatischen Ascomyceten entsprechen. In oder auf dem Stroma entstehen die Fruchtlager. . . . Bilden dagegen die Konidienträger ein festes palisadenartiges Lager, so erhalten wir die Conidienlager. Diese Conidien-

lager entstehen meist oberflächlich an einem Stroma oder innerhalb eines Stromas, indem der obere Teil desselben abgeworfen wird. Ein solches Conidienhymenium kann auch gefaltet sein, und die einzelnen Faltungen können Kammern in Stroma bilden. Wir erhalten dann ein Stroma mit unregelmäßigen Kammerräumen im Innern, die von dem Conidienhymenium ausgekleidet werden." He says of the pycnidium: "Endlich auch kann das Conidienhymenium in einem besonderen Gehäuse eingeschlossen werden. Wir nennen den so entstehenden Fruchtkörper dann Pyknide; dieselbe entspricht dem Perithecium der Pyrenomyceten." Quite obviously there is here a poor distinction between the definition of the stroma as "Gewebekörper" and "vegetativen Gebilden" and of the pycnidium as a "besonderen Gehäuse". This same ambiguity will be seen in most of the examples cited below where interpretation of "stroma" is attempted. de Bary (5, p. 246) says: "The pycnidia, like the perithecia, are according to the species either formed singly from the filamentous mycelium, or are placed in or on compound pycnidiophores (stromata)" while (l. c. p. 498) the "receptaculum" is defined as "same as stroma" and "in Ascomycetes, same as pycnidium". The ambiguity here lies in speaking of pycnidia as *single* or in *stromata* while a conceptaculum is given as a synonym of both pycnidium and stroma. Voges (102, p. 45) comes near to a lucid conception of stroma for he states: "Die Pyknide aber ist nichts weiter als eine besondere Ausgestaltung des Stroma in Form eines Gehäuses, das schützend das Hymenium umgibt." This bare statement, however, is not sufficient and besides it is marred by some of the untenable ideas he advanced, which have been discussed under *Hendersonia rubi*, and by his emphatic statement that the pycnidium can not be used for systematic purposes. Dodge (24, p. 755), in his studies with *Schizoparme straminea*, also came near the truth when he states that "on agar, however, several pycnidia may arise from one of these masses of plectenchyma in such a way as to suggest that the line separating such pseudoparenchymatous primordia from true stromata is not to be too sharply drawn." Vestergren (100, p. 10) too, brought out a valid objection when he stated ". . . scheint mir, rein morphologisch betrachtet, kein Grund dafür vorzuliegen, die mit einem einzigen Entleerungsporus versehenen gekammerten Fruchtkörper unter den *Sphaeropsideen* als Stromata anzusehen." Hesler (37, p. 66) describing the pycnidia of *Sphaeropsis* says that "they may be single, confluent, or united into a stroma" and this is evidently the same conception held by Taubenhaus (97) and by Harter and Field (36). (See p. 22.) von Höhnel (42, p. 261) has set forth quite clearly his viewpoint in the following words: "Bei vielen stromatischen Formen ist es zweifelhaft, ob sie wirkliche Pykniden haben, oder nur Lokuli im Stroma, also vielleicht zu den Stromaceen gehören" and (l. c. p. 265) "Auch betone ich, daß die Stromaceen zum Teil wenig ausgeprägte Formen sind, mit variablem Stroma, fließende Formen, die der Klassifikation große Schwierigkeiten

bereiten." However in his later key (50, p. 306) he defines a pycnidium as follows: „Gehäusewandung ringsum ziemlich gleich stark, außen und innen gut gegrenzt. Conidienhohlraum einfach, sehr selten unten mit Vorsprüngen nach innen (*Diplodia*-Arten)" while (l. c. p. 308) he describes the group which contains stromatic forms as "Fruchtkörper nicht gehäuseartig, mit einem oder mehreren Conidienhohlräumen oder oberflächlicher Conidienbildung. . . . Conidienbildung in geschlossenen Hohlräumen (Lokuli) im Gewebe. Lokuli einfach oder unvollständig geteilt gekammert, . . . Wandung meist sehr ungleichmäßig dick." Finally one should compare the statements of Stevens (93, h. 586) and Petrak (70, p. 212). Both deal with species of *Sphaeropsis*. The former shows that the stroma varies according to the nature of the substratum while Petrak has presented a minute description of the stromatic structure. The writer agrees with the observations of the first and therefore considers the description of the second to be rather futile.

After this review of the literature let us now consider further the data given in this paper to prove that the distinction between stromatic and non-stromatic pycnidia is untenable for the simple reason that all pycnidia are stromatic. That portion of a pycnidium, in *Phoma* for instance, which is ordinarily called the pycnidial wall is stroma, just as much so as the surplus tissue between the individual locules of such structures as found in *Botryodiplodia* or *Cytospora*. In the development of the *Phoma* pycnidium a single primordium is concerned but in the latter two cases several primordia are involved. When several primordia arise close together they become confluent, a brown envelope may form (i. e. in some species) around the entire mass of tissue and the structure then functions in the same manner as the simple pycnidium except that usually several cavities may arise within the structure(1). Such structures might be known as composite pycnidia as distinguished from the simple pycnidia, i. e. *Phoma*. This retains something of the original designation of Fries (28). Sometimes the cavities or locules remain distinct *(Botryodiplodia)* or again they may become confluent *(Cytospora)* to form a single irregularly chambered cavity. The tissue between the separate locules or chambers of any composite pycnidial structure is not a specially formed substance but is merely the remains of the primordial tissue which, depending upon the species or perhaps even on environmental conditions, has become brown, distorted, or changed in other ways. The entire tissue of the primordium is potentially spore forming but we have seen that the oxidizing process which browns the outer layers of cells renders that portion useless for the purpose. Also in the cases of arrested development there is often a wide layer of unused hyaline tissue between the cavity and the outer brown envelope. Sometimes the development is arrested even before the cavity

(1) Bauke (6) reports the same thing for *Pycnis Cucurbitariae elongatae.*

forms and such structures are commonly reported in the literature as sclerotia. The fruit body, in some species, remains partially erumpent and then disintegrated portions of the substratum, quite often, are to be found intermixed with the stroma, as in *Phomopsis*, *Cytospora*, *Micropera*, *Naemosphaeria*, etc. The presence of this partially disintegrated substratum often obscures the limits of the stroma, especially in younger stages before the woody elements are completely dissolved.

Ruhland (79, p. 47) has described, for *Valsa nivea*, the manner in which the pycnidial primordia arise and become confluent to form a single fruiting structure with many locules and to this type he has applied the term "polythalame". He mentions (l. c.) under a footnote that "Die Details bez. einer etwaigen symphogenen oder meristogenen Entstehung der ersten Anlagen können nur mittels besonderer Reinkulturen gelöst werden. Für uns ist diese Frage ohne weiteres Interesse." Most certainly the matter is of more than secondary interest if we are to give proper interpretation to the developmental morphology of these composite fruit bodies and to the stroma. Ruhland (l. c. p. 72) has stated that "Das Stroma ist in seiner primitivsten Ausbildung nichts weiter als reichliche Myzelanhäufung, ...", and further (l. c. p. 73) that "Das Entostroma nimmt seinen Ursprung unmittelbar aus dem Mycel, . . . Das Ectostroma ist ein unmittelbares Produkt des jugendlichen Entostromas, . . ." and to this is added (l. c. p. 75) that "Die Pyknide nimmt ihren Ursprung meist von kugeligen Anlagen aus, kann aber auch spontan durch Lückenbildung in der Ectostromasubstanz entstehen." Since Ruhland has not observed the early stages of primordial formation (cf. footnote, l. c. p. 47) it is evident that he can not say that the stroma is the mere result of the massing of mycelium. More correctly the statement should be that the stroma is the product of the proliferation of hyphae after the formation of a distinct primordium. All evidence obtained by the writer from studies of the initial stages of pycnidial fruit bodies points to this conclusion.

Discussion of systematic characters. It is clear that spore characters are, on the whole, quite reliable and therefore should be employed as far as possible in any scheme of classification. Certain pycnidial characters, such as texture of tissue, and presence or absence of ostiole perhaps have taxonomic importance but only for smaller units, as between genera or species. The shape and color serve better for larger subdivisions but even here one must bear in mind that certain genera, i. e. *Septoria* and *Hendersonia*, may have hyaline pycnidia under one set of conditions and brown under another set. The writer suggests the use of the terms simple and composite pycnidia. They should serve a good purpose if used judiciously. The terms correspond to a certain extent with the general conceptions of non-stromatic and stromatic, which have been applied universally in a loose and ambiguous manner by the majority of mycologists.

There always will be difficulty in subjecting living organisms to the harness of a systematic key. This is due partly to our incomplete knowledge, and partly to morphological variability of certain species, but perhaps more to the fact that most of our systematic structures are erected too soon and on too few basic characters. As Voges (102, p. 43) has adequately stated: "Eine einzelne Eigenschaft des Organismus, mag sie auch noch so auffällig vor allen anderen hervortreten, kann nicht für dessen Stellung im System bestimmend sein. Nur die Summe jener Eigenschaften, woraus sich eben die Wesenheit der Art und des Individuums zusammensetzt, in ihrer Totalität, der Gesamthabitus der jeweiligen Pilzform ist maßgebend für die Einreihung im System." This applies particularly to our knowledge concerning connections between the ascus and conidial stages. It is difficult to formulate any satisfactory plan of classification for the *Sphaeropsidales* because they are only related fruit forms of the Ascomycetes. There is, of course, reciprocal application of this statement to the Ascomycetes. Even if we could be certain that each species in the Ascomycetes had a single related species in the *Sphaeropsidales* the classification would still be difficult but we must consider that some species of Ascomycetes have several related imperfect stages (cf. Klebahn 57, p. 30, Shear and Dodge 85, etc.). More than this we find, without reference to the perfect stage, even among the *Sphaeropsidales* that mere developmental stages have been considered as genera, for example in *Sphaeropsis*, *Septoria*, *Rhabdospora*, etc. As a matter of fact von Höhnel (39, p. 248—249) has sanctioned the acceptance of such genera for the mere sake of convenience. It comes then to the question of which shall be subordinated, the species or the scheme of classification? There are advantages, to be sure, in subordinating the species, but surely scientific principles demand that a specific name represent a living entity. If we sacrifice these principles then we must expect a generic name for each development stage of a fungus, or we might even say for each spore form, i. e. *Macrophoma*, *Sphaeropsis*, *Diplodia*. Surely there is no need of such a procedure. We already have too many poorly defined genera; the better plan is to retain a single specific name for a single species in so far as our knowledge permits. If we apply our new conceptions, obtained by thorough investigation, to each group of fungi we shall gradually eliminate superfluous species and genera. Thus we will attain a more perfect and natural system of classification.

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Explanation of Plates (1).

Plate 1. Septoria lycopersici.

Fig. 1. A young pycnidium buried in the agar (upper right), with only the upper half oxidized to form a definite brown wall.

„ 2. Pycnidium on surface of agar (upper left), with definite thick brown wall and with a few traversing hyphae. Before gelatinization.

„ 3. Pycnidium just below the surface of the agar (lower left). The lower portion of the wall is not distinct. The contents consist of a vacuolated gelatinous substance, which represents the condition just before spore formation.

(1) All the photomicrographs were taken with the same lens combination and all have been equally reduced. Fig. 1, Plate 5 is the only exception. This was taken with a higher power of magnification. The approximate diameter of this fruit body is 600 μ. For comparison, the diameter of the fruit body in Plate 2, fig. 3 is 250 μ.

Plate 2. Phomopsis arctii and P. coneglanensis.

Fig. 1. *P. arctii.* Three fusing primordia in clover stem, with a common brown, encircling layer.
„ 2. Ditto. Later stage. Cavity formation has taken place at the center.
„ 3. *P. coneglanensis.* Pycnidium in agar. Cavity formation occuring along a line of cells, evidently by lysigenetic action. (Vide text fig. 3.)

Plate 3. Phomopsis coneglanensis.

Fig. 1. Small primordium disrupting clover stem tissues.
„ 2. Fusing primordia. Cavity formation has occured in the central portion.

Plate 4. Cytospora minuta.

Fig. 1. Three primordia. The two at the right are becoming fused.
„ 2. Older stage of fusion.
„ 3. Still later stage. Elongation has taken place and the loose projecting hyphae above indicate the mode of enlargement in this type of primordium. (Vide text fig. 4 for further development; also text fig. 5.)

Plate 5. Sphaeropsis gallae and S. glandulosa.

Fig. 1. *S. gallae.* Composite fruit body in agar. The small cavity (lower left) shows vacuolated contents. The large cavity is surrounded by a meristematic layer. (Vide text fig. 8 for early stages; also text fig. 7.)
„ 2. *S. glandulosa.* Young primordia below the surface of the agar. Various degrees of development and of fusion are to be found. In these immersed structures no brown outer layer is formed.
„ 3. Ditto. Showing more complete fusion of primordia at surface of agar and also the formation of a definite brown outer layer.
„ 4. Ditto. Fruit body in clover stem. This structure evidently arose from several primordia. The cavity formation occurred at several points but later became confluent. (Vide text fig. 6.)

Plate 6. Micropera caespitosa.

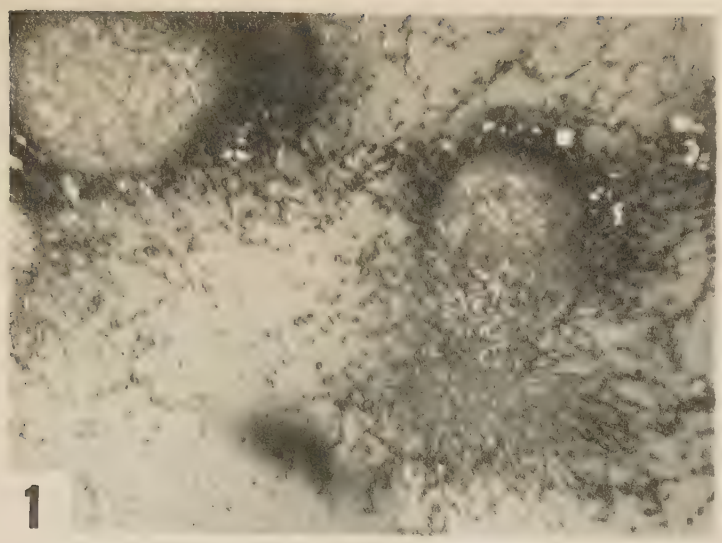
Fig. 1. Three primordia (above) arising in the tissues of a clover stem.
„ 2. When several primordia become confluent there is formed an extensive mass of fungous tissue.
„ 3. Later stage. Spore cavities form at different points. (Vide text fig. 13.)

Plate 7. Micropera drupacearum.

Fig. 1. A fruit body with a large cavity. Slightly below and to the left there is seen a small differentiated area. This represents the initial stage in the formation of a second cavity.
„ 2. A mature fruit body which has broken open at the top. (Vide text fig. 14 and 15.)

Plate 8. Micropera spuria.

Fig. 1. Early stage in formation of primordium.
„ 2. Vertical elongation of primordium by means of proliferation of hyphae at the top.
„ 3. Final development of cavity at the apex. (Vide text fig. 16.)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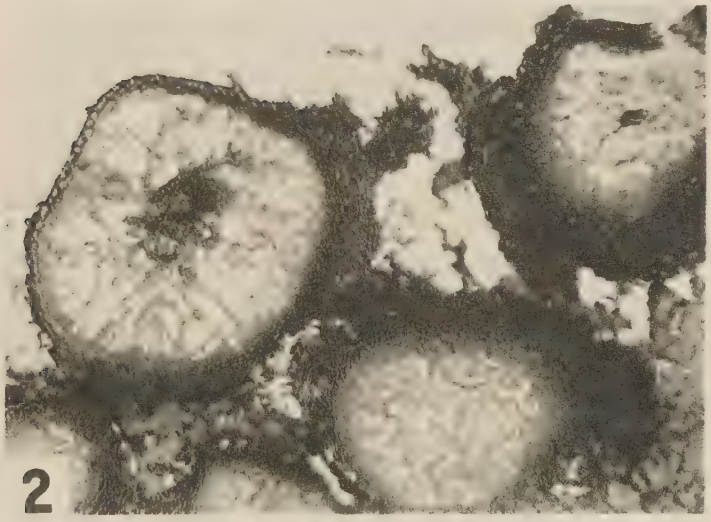
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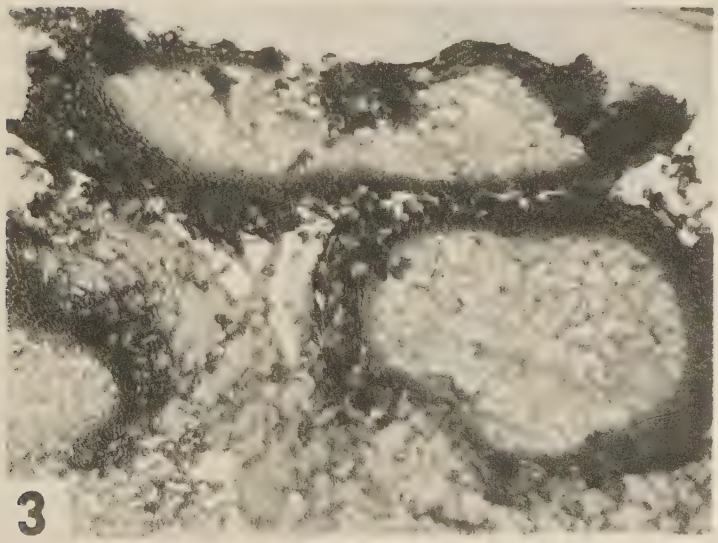
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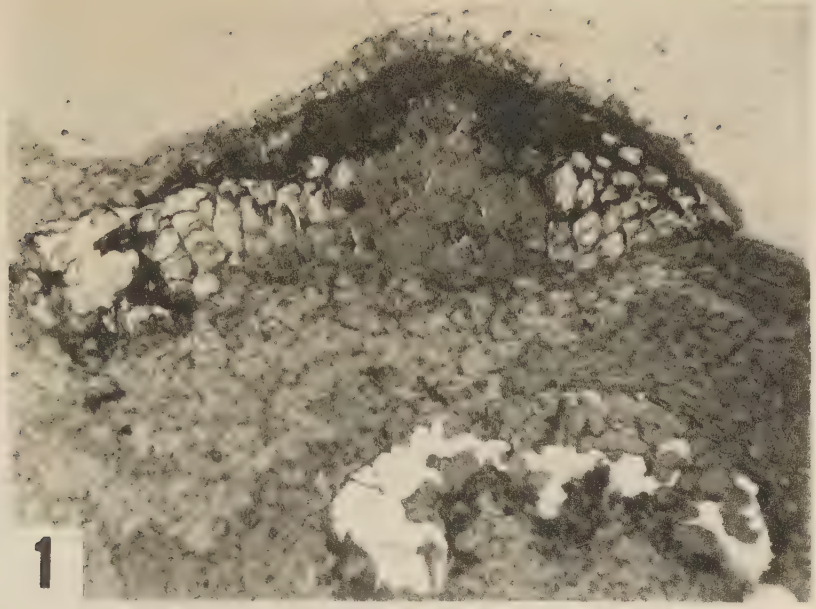
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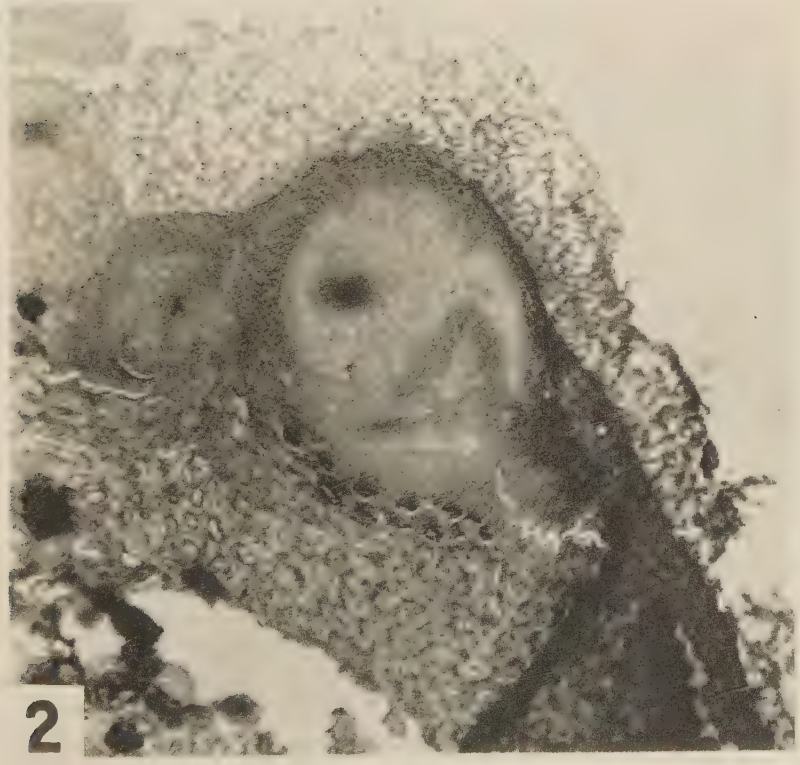
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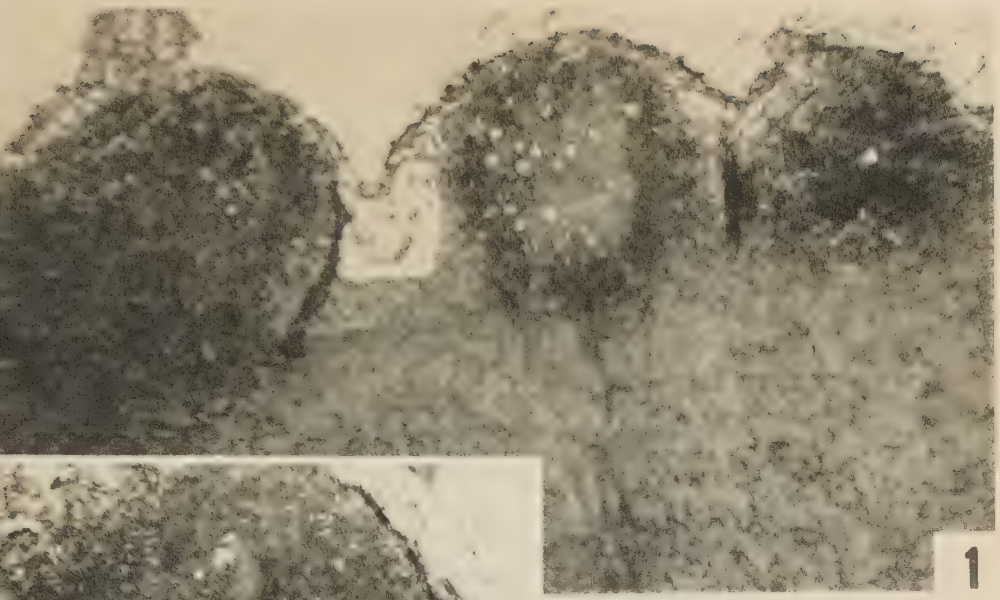

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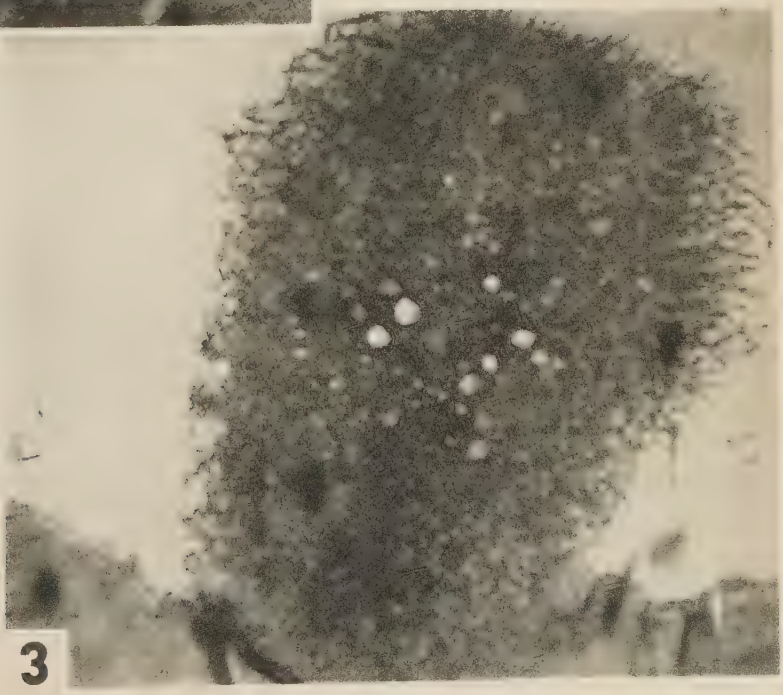

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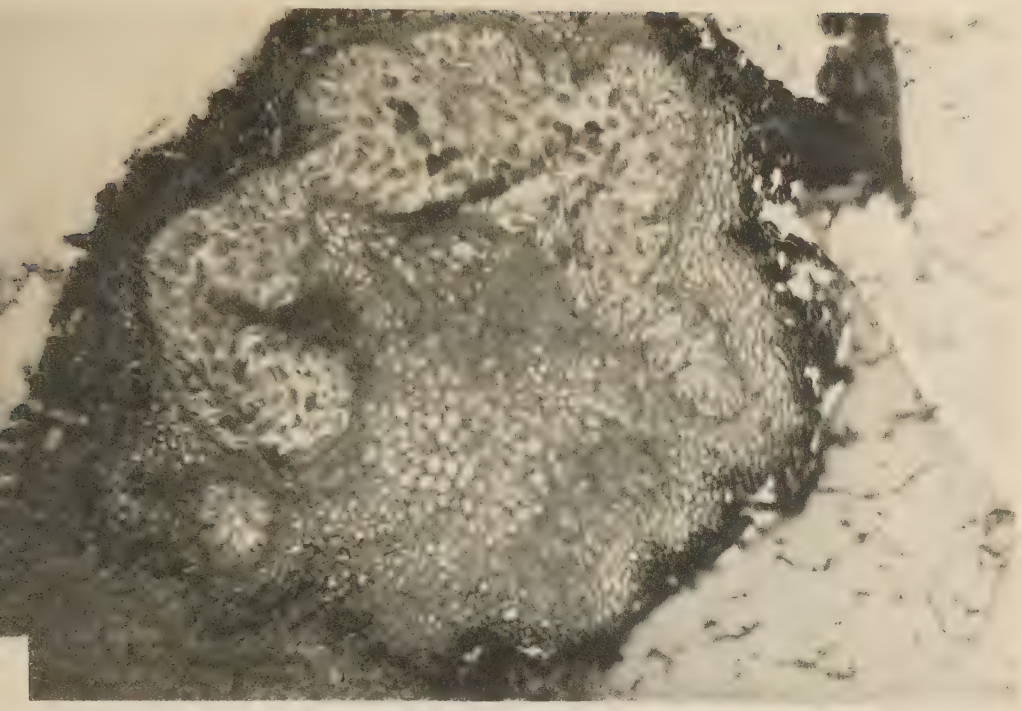

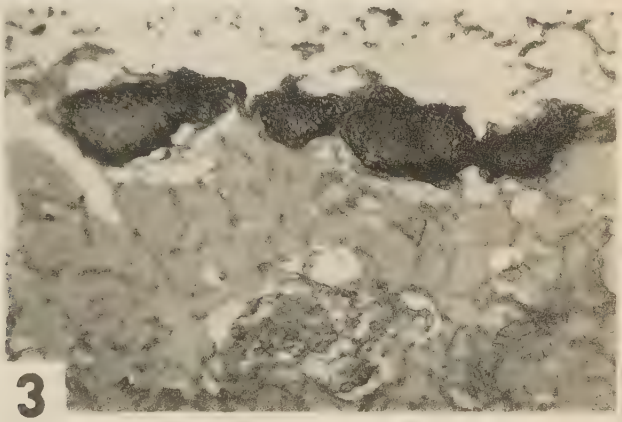

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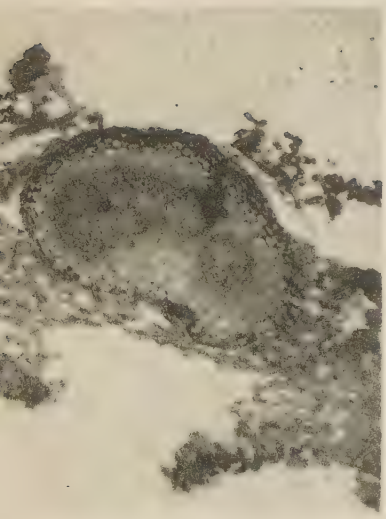

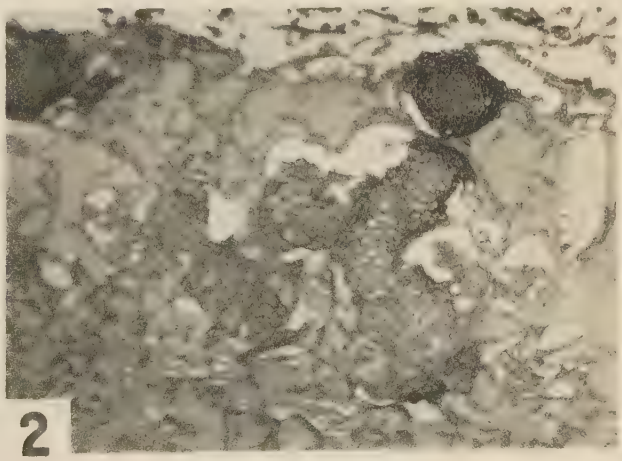

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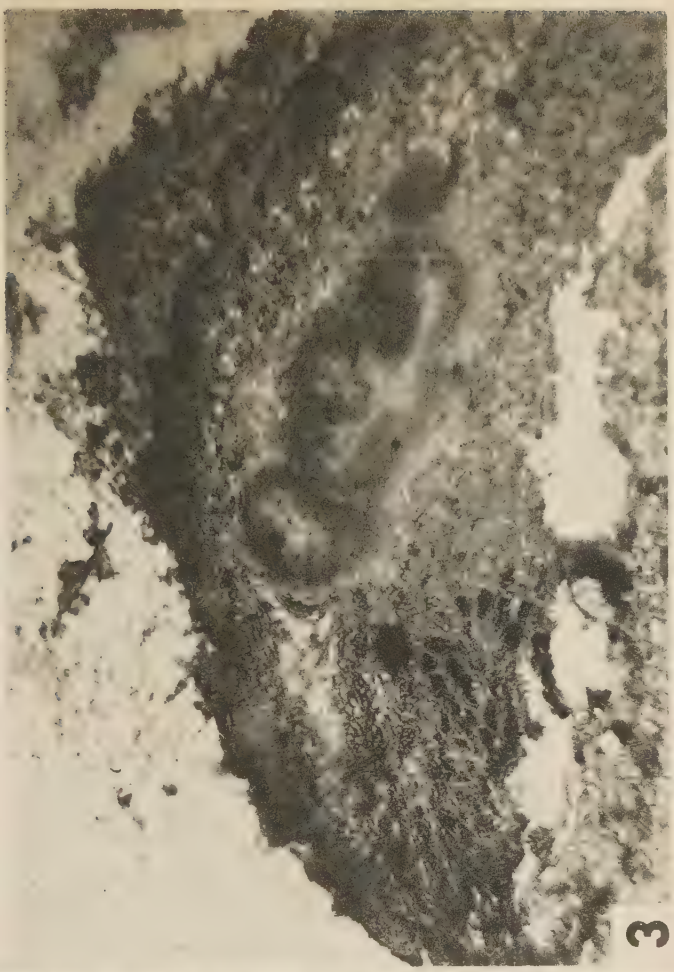

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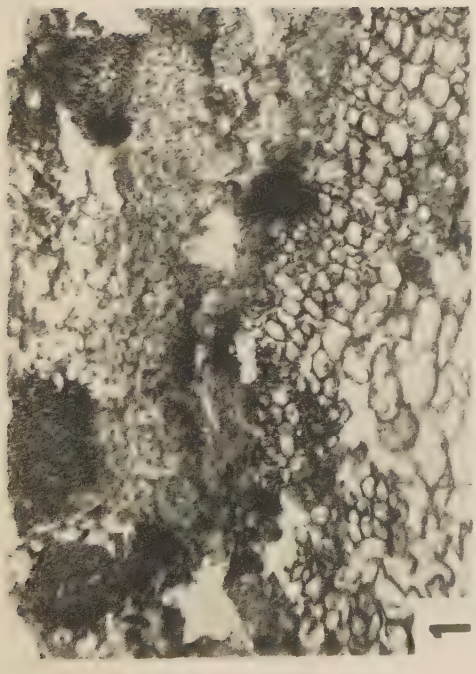

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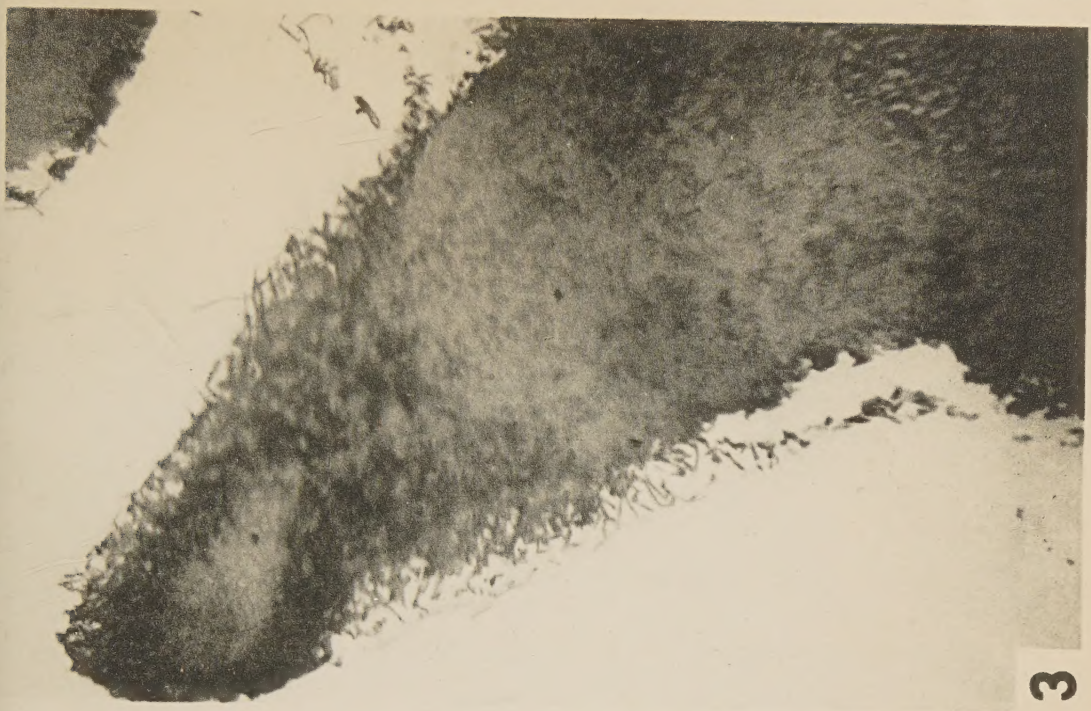
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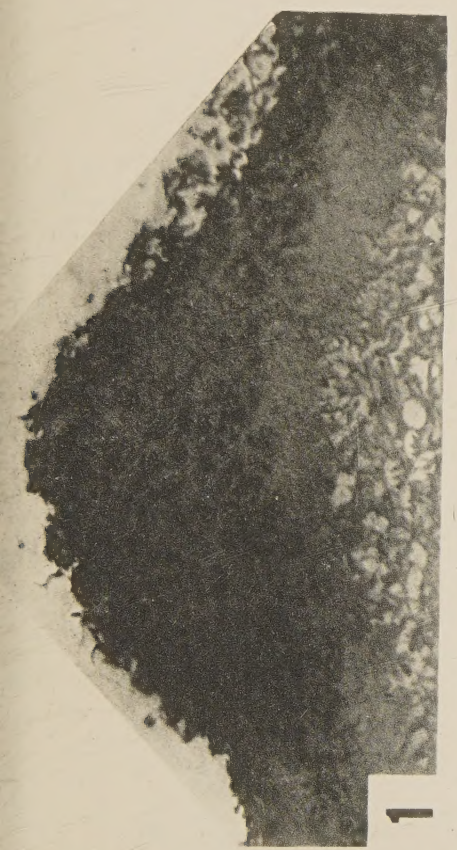
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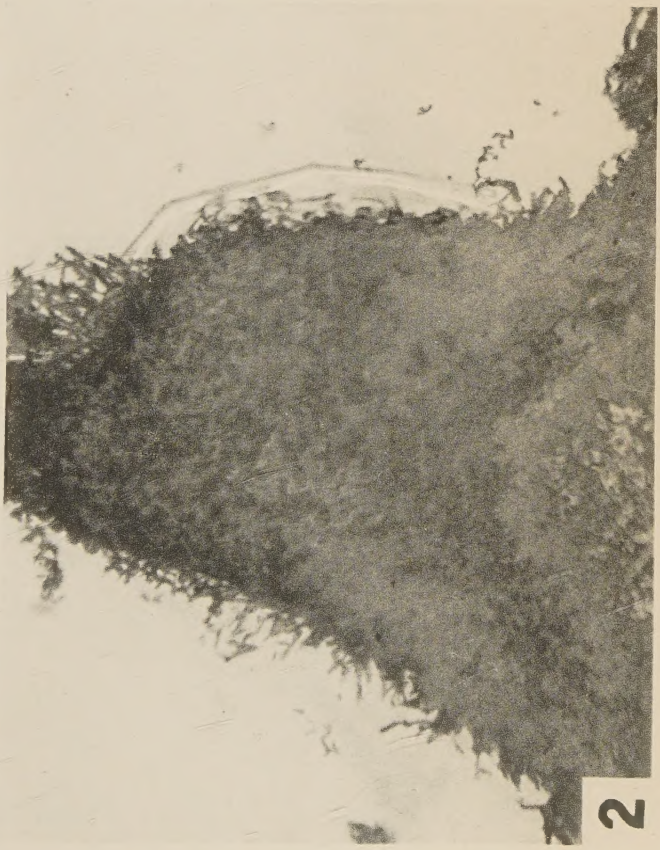
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